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REVISION OF THE MARSUPIAL GENUS *PLANIGALE* TROUGHTON (DASYURIDAE)

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ABSTRACT

Planigale Troughton, 1928 is revised and a new generic diagnosis provided. Five species are recognized: *P. ingrami* (Thomas, 1906) (including the forms *subtilissima* Lönnberg, 1913, and *brunnea* Troughton, 1928); *P. tenuirostris* Troughton, 1928; *P. gilesi* Aitken, 1972; *P. maculata* (Gould, 1851) (formerly regarded as a species of *Antechinus* Macleay, 1841 and including the form *Phascogale minutissima sinuatis* Thomas, 1926); and *P. novaeguineae* Tate and Archbold, 1941. These species are placed in three groups: the *P. maculata* group, the *P. ingrami* group, and the *P. gilesi* group. *P. gilesi* is regarded as the most specialized species, having completely lost the last upper and lower premolar. Two additional forms of *Planigale* noted, one from northwestern Western Australia and another described by Lundelius and Turnbull (1973), may represent additional species.

The genus *Planigale* is considered to be related to *Ningaui* Archer, 1975 as well as to some *Antechinus*-like dasyurids such as *Phascogale* Teminck, 1824. There is also some affinity with *Sminthopsis* Thomas, 1888, but the common features that some species of these two genera share may be the result of convergence in arid adaptation.

In 1928 Troughton proposed that *Phascogale subtilissima* Lönnberg and *P. ingrami* Thomas should be included with *Planigale tenuirostris* Troughton in the genus *Planigale*. Subsequently, *Planigale novaeguineae* Tate and Archbold and *Planigale gilesi* Aitken were described. The placement of *maculatus* Gould in *Antechinus* by most modern authors (e.g. Tate 1947, Ride 1970) is anomalous. Archer (1975) considers it to be within *Planigale*.

Some non-*Planigale* species (in *Antechinus*) exhibit characters previously believed confined to *Planigale*—in particular, flatheadedness (Ride 1970)—while inclusion of *P. novaeguineae* and *P. gilesi* in *Planigale* indicates that not all *Planigale* are minute in size. Minute dasyurids are now known to occur in another dasyurid genus, *Ningaui* Archer. These developments in classification and taxonomy emphasize the need for revision in the genus *Planigale*.

METHODS

Cranial measurements are given in Table 1. The method of taking measurements is shown in Figure 1. Characters of particular importance in differentiating species of *Planigale* are nasal lengths, widths, contact between premaxillae and

nasals, distance between posterior lacerate foramen and anterior edge of alisphenoid bulla (or tympanic wing), transverse distance across foramen magnum, and skull depth in front of alisphenoid bullae. Similarly, external measurements were made of the ear (from notch to tip of pinna), supratragus (maximum length), nose-vent (anus), tail-vent, and hind foot (less claws). Unless otherwise noted, measurements were made on preserved materials from which skulls had already been removed. External measurements should not be considered directly comparable with measurements of fresh material (e.g. Lidicker and Marlow 1970).

Some small dasyurids have distinctive morphological dental and cranial characteristics. Within genera, such as *Sminthopsis*, these characteristics are sufficiently constant to diagnose species. In other genera, such as *Planigale*, these distinctive morphological characters are less common. Only *Planigale gilesi* in lacking P4 is obviously and consistently distinct from other species. Recognition of other species of *Planigale* requires examination of size and consideration of relative cranial and dental proportions. A statistical summary of absolute size in species of *Planigale* is given in Table 1. A summary of cranial, dental, and external proportions, as ratios, is given in Table 2.

These ratios are as follows:

1. Basicranial length/zygomatic width (BL/ZW): an estimate of brachycephaly;
2. Minimum inter-orbital width/ZW (IO/ZW): an estimate of relative mid-cranial frontal restriction;
3. Alisphenoid bullae width (left and right combined)/ZW (BW/ZW): an estimate of relative width of alisphenoid bullae;
4. BW/ M^{1-3} : an estimate of alisphenoid bullae width relative to M^{1-3} length;
5. Bullar length (measured from posterior lacerate foramen to anterior edge of expanded alisphenoid bulla/ M^{1-3} (BL/ M^{1-3}): an estimate of relative length of periotic and alisphenoid bullae (or tympanic wing) inflations;
6. Skull depth (measured vertically immediately anterior to alisphenoid bullae)/ZW (SD/ZW): an estimate of relative depth of skull;
7. SD/BL: an estimate of skull depth relative to skull length;
8. SD/($C^1 - M^4$): an estimate of skull depth relative to length of cheek-tooth row;
9. SD/IO: an estimate of skull depth relative to mid-cranial restriction;
10. Foramen magnum diameter (maximum transverse)/SD (FM/SD): an estimate of relative size of foramen magnum;
11. M^{1-3} /ZW: an estimate of width of skull relative to M^{1-3} length;
12. ($C^1 - M^4$) — ($M^1 - M^4$)/(M^{1-3}) ($= C^1 - P^4/M^{1-3}$ in Table 2): an estimate of length of ($C^1 - P^4$) relative to M^{1-3} length which is also an estimate of relative cheek-tooth row crowding;
13. ($I_1 - M_4$) — (M_{1-4})/(M_{1-3}) ($= I_1 - P_4/M_{1-3}$ in Table 2): an estimate similar to 12 above, but for lower teeth and involving lower incisors;
14. Nasal length (maximum)/BL (NL/BL): an estimate of relative length of nasals;
15. Nasal width (maximum across both nasals)/ZW (NW/ZW): an estimate of relative width of nasals;
16. NW/NL: an estimate of relative length and width of nasals;
17. Premaxillary-nasal suture/NL (PN/NL): an estimate of relative length of premaxillary-nasal suture;
18. Minimum distance between premaxillary and maxillary vacuities/BL (VV/BL): an estimate of relative palatal evacuation;
19. Dentary length (from posterior edge articular condyle to anterior edge of I_1 alveolus)/BL (DL/BL): an estimate of relative length of dentary;

20. Tail-vent length/head-body length (TV/HB): an estimate of relative length of tail;
21. Hind foot length/HB (HF/HB): an estimate of relative length of foot;
22. Length of supratragus of ear/ear height from notch (ST/E): an estimate of supratragus length relative to ear height.

These ratios were selected following an overall examination of specimens which indicated that although there were apparent differences in cranial structure, expression of some of these was confused by differences in relative size. As a result, ratios were computed using absolute measurements for each specimen. Means of these ratios were then obtained.

Cranial, dental and external terminology is that used by Archer (1975, 1976). Abbreviations for specimen numbers unless otherwise indicated are as follows: AMNH, American Museum of Natural History; BM, British Museum (Natural History); C, National Museum of Victoria; D, Victorian Fisheries and Wildlife Department; JM or J, Queensland Museum; B, Butler collection in the Western Australian Museum; 67.8.73, example of number in fossil collection, Western Australian Museum; NTM, Northern Territory Museum. The following institutions all have *M* as a prefix to their mammal specimens. To distinguish them, a prefix indicating the institution has been added to the number as follows: AM *M*—, Australian Museum; SAM *M*—, South Australian Museum; WAM *M*—, Western Australian Museum.

Family DASYURIDAE

Genus *Planigale* Troughton

Planigale Troughton, 1928, p. 282.

TYPE SPECIES: *Planigale ingrami brunneus* Troughton, 1928, by original designation. (Not *P. ingrami* Thomas, 1906, as cited by Tate 1947, and Laurie and Hill 1954).

DIAGNOSIS

Dasyurids smaller than *Antechinus*, and differ from these in having extremely reduced maxillary vacuity; very small paracone on M^{1-3} and small talonids on M_{1-3} . Differ from *Sminthopsis* and *Antechinomys* Krefft, 1867 in possessing straight uncurled external edge on supratragus of ear; short, broad pentadactyl hind foot; enlarged metatarsal granules; nasals broadened posteriorly; apparent lack of squamoso-frontal contact on external surface of skull; posterior cingula present M^{1-3} ; reduced protocone and paracone on M^{1-3} ; reduced talonid on M_{1-3} ; P_4 single-rooted or

absent; palatine vacuity lacking. Differ from *Nin-gau* in possessing very broad hind foot: straight uncurled external edge of supratragus of ear; posterior cingula on M^{1-3} ; nasals markedly broadened posteriorly; no palatine vacuities.

DESCRIPTION

Tail thin without brush or crest and approximately equal to, or longer than, nose-vent length.

Supratragus of ear with straight external edge. Helix curls beneath root of supratragus. Anterior edge of tragus bears short hairs. Up to two fold lines for retraction of pinna. Notch on posterior edge of pinna variably present.

Mystacial vibrissae on each side in 6–7 ill-defined rows with 2–6 vibrissae in each row; 1–3 supra-orbital vibrissae; 6–8 genal vibrissae; 3–4 carpal vibrissae.

Hindfoot broad with 7 post-digital pads including 3 interdigital, 1 hallucal, 1 post-hallucal, 1 anterior and 1 posterior outer metatarsal pad. All pads with apical granules appearing transversely striated, although striae do not normally exist as physical ridges on surface of granules. Sole naked except near heel. Hallux clawless.

Palage generally lacks distinctive markings. Abnormal variation includes spots.

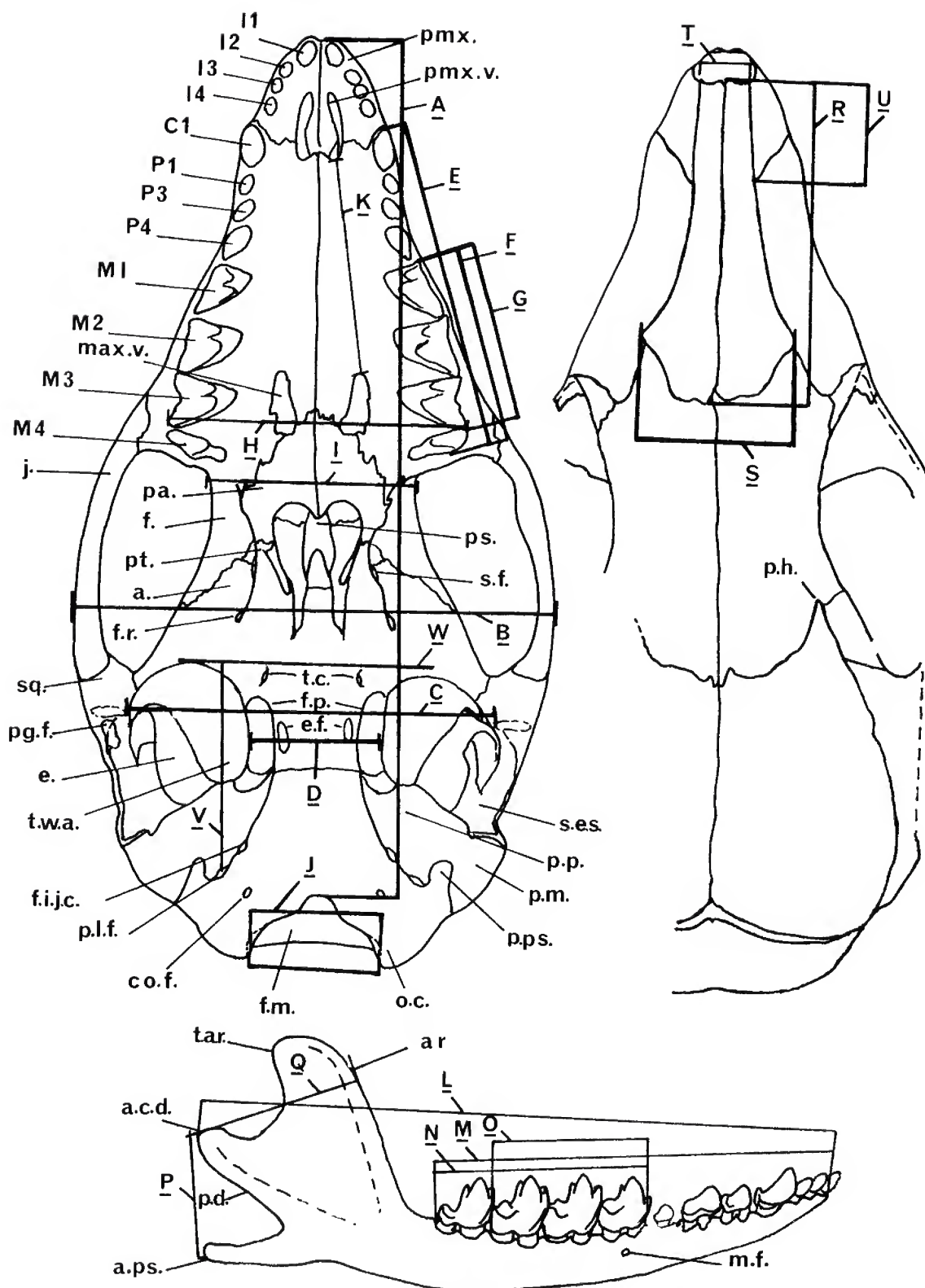
Median groove pronounced and to top of rhinarium. Groove demarcating whole of external rim of rhinarium. Nostrils centrally situated on each side.

Five to twelve nipples have been noted in this study. Fleay (1967) records fifteen juveniles attached to one female *P. maculata* (as *P. ingrami*).

Nasals broadly widened posteriorly. Premaxillary-nasal contact shorter than maxillary-nasal contact. Lacrimal foramen on rim of orbit or just anterior to it. Infra-orbital foramen opens onto surface of maxilla without contact with jugal. Postorbital process on frontal absent. Prominent venous foramen in frontal on dorsal rim of orbit. Contact between squamosal and frontal apparently lacking on outside of skull. Variably developed, anterior, dorso-lateral extensions (horns) of squamosal and parietal present. Postero-mesial edge of palatine at point of contact with frontal in orbit extremely variable in shape. Cranium flattening reasonably constant intraspecifically but various interspecifically. Premaxillary vacuity short, not extending posteriorly beyond posterior edge of canine alveolus. Maxillary vacuity very short not exceeding length of premaxillary vacuity. Palatine vacuity lacking. Postero-lateral palatal vacuity lacking or so incomplete as to be barely suggested. Posterior palatal

spine generally not well-developed. Pterygoid with spinous hamular process. Alisphenoid tympanic wing poorly developed with short periotic contact. Periotic with low, variably enlarged tympanic wing. Ectotympanic large with only small portion covered by alisphenoid tympanic wing. Transverse canal of basisphenoid very small to absent (or indistinguishable) from anterior end of foramen pseudovale. Variably developed entocarotid canal adjacent to elongate narrow foramen pseudovale. Opening of eustachian canal large. Internal jugular canal enclosed in tube formed by basioccipital and periotic. Tiny posterior lacerate foramina variable in number and antero-mesial to paroccipital process. Condylar foramina tiny to large and variable in number (includes hypoglossal foramen). Paroccipital process barely inflated as continuation of anterior tympanic wing of periotic. Stapes columnar, but generally (perhaps universally) with very tiny stapedial depression near contact of foot plate with columella. Depth of dentary ventral to teeth variable. Masseteric fossa wide. Mandibular foramen beneath M_1 or M_2 .

I^1 largest incisor and separated from I^{2-4} by diastema. I^{2-4} incisor crown length and height variable but I^3 generally highest. C^1 tallest crown in upper dentition. Base of C^1 enamel crown often far above alveolar rim with tiny posterior cuspule and barely distinguishable to absent buccal and lingual cingula. P^4 , when present, largest upper premolar. P^1 never larger than, but sometimes subequal to, P^3 . Small posterior cuspule on P^{1-4} sometimes absent. Cingulum around P^{1-4} generally entire. Paracone very reduced and close to metacone of M^{1-3} . Paracone increases in height from M^{1-4} . Basal antero-posterior length of protocone decreases from M^{1-4} . Tiny protoconule variably present on M^{1-3} . No metaconule on M^{1-4} . Preproto-crista continuous with anterior cingulum, which is complete on M^{1-4} . Postproto-crista continuous with posterior cingulum on M^{1-3} which extends buccally for approximately two-thirds posterior length of each molar. Prefossa tilts postero-buccally and not enclosed posteriorly except by posterior cingulum of M^{1-3} . Metacone absent on M^4 . Paracrista of M^1 variably reduced to absent. Paracrista of M^{1-4} increases in length posteriorly. Metacrista of M^2 never shorter than metacrista of M^1 and M^3 . Styler cusp A not clearly distinguishable on any molar, possibly homologous with part of antero-buccal cingulum of M^1 . Styler cusp B of M^1 often completely indistinguishable and may be totally reduced or fused with paracone. Styler cusp B, as defined by buccal edge of paracrista, present on M^{2-4} but largest in M^{2-3} . Styler cusp C tiny, only variably present on posterior flank of styler



cuspid B or anterior flank of stylar cusp D of M^{2-3} . Stylar cusp D large on M^{1-2} , tiny on M^3 . Stylar cusp E tiny to absent on M^{1-3} . Generally, where stylar cusps C and E tiny to absent, buccal fossae of each molar tilt buccally and are not enclosed on either side of stylar cusp D. Ectoflexus greatest in M^3 and decreases anteriorly. Buccal length of M^{1-4} decreases posteriorly. Anterior width of M^{1-3} increases posteriorly with M^4 anterior width never greater than that of M^3 . I_1 crown taller and longer than I_2 . I_2 taller and longer of subequal to I_3 . Small posterior cingular cusp on $C_1 - P_4$ variably developed or absent. Buccal and lingual cingula developed on $C_1 - P_3$ not generally complete at anterior edge. Development of cingula on P_4 varies with size of tooth. C_1 widest antemolar tooth. P_4 varies from absent to peg-shaped to oval. When P_4 present, generally single-rooted but rarely double-rooted. Protoconid considerably largest trigonid cusp of M_{1-4} . Metaconid height of M_{1-3} exceeds paraconid, but smaller or subequal to paraconid of M_4 . Difference between paraconid and metaconid decreases posteriorly in M_{1-3} . Middle of protoconid posterior to middle of buccal side of trigonid root. Hypoconid decreases in height posteriorly in M_{1-4} being absent or miniscule on M_4 . Entoconids tiny to absent on M_{1-4} but when present most noticeable on M_2 . Variable tiny to absent parastylid on buccal opening of trigonid. Variable tiny to absent metastylid on postero-buccal edge of metaconid. Conspicuous anterior cingulum on M_{1-4} but may be only partly developed on M_1 . Lingual confluence of posterior cingulum and posterior hypocristid defines hypoconulid. Prominent hypoconulid notch in anterior cingula of M_{2-4} . Well-developed carnassial notch between protoconid-paraconid and protoconid-metaconid but, generally, carnassial groove very tiny to absent. Talonid wider than trigonid of M_1 , narrower or subequal to trigonid of M_2 , and progressively narrower than trigonid of

M_{3-4} . Paracristid M_3 longer or subequal to that of M_2 which is longer than paracristid of M_4 which is longer than paracristid of M_1 . Metacristid of M_{2-3} subequal and larger than paracristid of M_4 which is larger than that of M_1 . Posterior hypocristid of M_2 longer than that of M_1 and subequal to that of M_3 .

GENERIC DISCUSSION

Troughton's (1928) concept of *Planigale* is based on the relatively flat-headed forms, *P. tenuirostris* and the *subtilissima* and *brunnea* forms of *P. ingrami*. As a result, he considers flat-headedness an important characteristic of the genus. Although *P. maculata* and *P. novaeguineae* have relatively less-flattened skulls, other dental and cranial characters are the same as in other species of *Planigale* and quite unlike any other dasyurid genus. Thus flat-headedness is not maintained as constant in *Planigale*. Flat-headedness probably enables the individual to squeeze into narrow crevices as suggested by Troughton (1967), Walker (1967) and others, and permits use of the head as an efficient wedge to raise objects, such as stones or bark, covering insects. Many dasyurids, including *P. maculata* and the *subtilissima* form of *P. ingrami*, studied in captivity use their heads for this purpose. Some *Antechinus* are also flat-headed (Ride 1970, Archer and Calaby in preparation), indicating that this adaptation has developed in more than one dasyurid lineage.

Species of *Planigale* generally lack an external squamosal-frontal contact. Exceptions are presumably abnormal. For example, in a specimen of *P. gilesi* (AM M7393) the left side of the skull shows clear exclusion of a squamosal-frontal contact, while the right squamosal may just contact the frontal. The bones are semi-transparent rendering identification of sutures difficult, and internal suture relationships may be apparent on the outside. These bones overlap rather than directly

FIG. 1: Terminology and mensuration in the skull and dentary of *Planigale* (based on *P. maculata*). *a.*, alisphenoid; *a.c.d.*, articular condyle of dentary; *a.ps.*, angular process; *ar.*, anterior border of ascending ramus; *co.f.*, condylar (and/or hypoglossal) foramen; *e.*, ectotympanic; *e.f.*, entocarotid foramen; *f.*, frontal; *f.i.j.c.*, foramen for internal jugular canal; *f.m.*, foramen magnum; *f.p.*, foramen pseudovalve; *f.r.*, foramen rotundum; *j.*, jugal; *max.v.*, maxillary vacuity; *m.f.*, mental foramen; *o.c.*, occipital condyle; *pa.*, palatine; *p.d.*, posterior border of dentary; *pg.f.*, postglenoid foramen; *p.h.*, parietal horn; *p.l.f.*, posterior lacerate foramen; *p.m.*, mastoid part of periotic; *pmx.*, premaxilla; *pmx.v.*, premaxillary vacuity; *p.p.*, petrosal part of periotic; *p.ps.*, paroccipital process; *ps.*, presphenoid; *pt.*, pterygoid; *s.e.s.*, squamosal epitympanic sinus; *s.f.*, sphenorbital fissure; *sq.*, squamosal; *t.a.r.*, tip of ascending ramus; *t.c.*, transverse canal; *t.w.a.*, tympanic wing of alisphenoid; *A-V*, positions from which cranial measurements were made: *A*, basicranial length; *B*, maximum zygomatic width; *C*, outside bullar distance; *D*, inside bullar distance; *E*, C^1-M^4 ; *F*, M^{1-4} ; *G*, M^{1-3} ; *H*, LM^3-RM^3 ; *I*, interorbital width; *J*, maximum width of foramen magnum; *K*, interpalatal vacuity distance; *L*, dentary length; *M*, I_1-M_4 ; *N*, M_{1-4} ; *O*, M_{1-3} ; *P*, tip of angular process to articular condyle; *Q*, articular condyle to anterior border of ascending ramus; *R*, maximum nasal length; *S*, maximum nasal width; *T*, minimum nasal width; *U*, nasal-premaxillary suture length; *V*, bullar length; *W*, line to which *V* is measured and represents antero-most level of alisphenoid tympanic wing.

abut, so that while they may not contact outside the skull, they may do so inside. A similar situation occurs in WAM M2846, a specimen of the *subtilissima* form of *P. ingrami*, where both sides are in doubt.

All generic characters given as diagnostic are separately shared with at least one other dasyurid genus, and no single character can be considered unequivocally diagnostic of *Planigale*. As with *Ningaui* (Archer 1975), it is to be expected that distribution among other dasyurids of characters found in *Planigale* will in part reveal intra-familial relationships.

It has been suggested that *Planigale* is a derivative of an *Antechinus*-like dasyurid (e.g. Troughton 1967, Ride 1970). The narrow molars, non-transversely orientated hypocristids, lack of palatine vacuities, wide nasals, apparent lack of squamosal-frontal contact on the outside of the cranium, wide feet, and short ears, are characters of *Antechinus*-like dasyurids such as *Phascogale*, but are not characters of the genus *Sminthopsis*. *Ningaui* provides a structural link between *Planigale* and *Sminthopsis*. This link is further suggested by *S. ooldea*, which exhibits mild paracone and talonid reduction, features well-developed and characteristic of *Ningaui* and *Planigale*. In general, species of *Planigale* appear most similar to *Ningaui*, *Antechinus*, and *Phascogale*, but also distantly similar to *Sminthopsis*. Direct similarity to *Sminthopsis* is minimal and involves characters which may be arid-adaptations achieved independently in *Sminthopsis* and *Planigale*.

Development of widespread arid habitats in Australia may have resulted in independent development of arid-adapted characters in several *Sminthopsis* and *Antechinus* species groups and in other dasyurids such as *Dasyercus* Peters, 1875 and *Dasyurides* Spencer, 1896. Some presumably arid-adapted characters are small body size, relatively short premolar rows, high-crowned teeth, dolichocephaly, and well-fenestrated palates. All except the last two are characteristic of *Planigale*, and some species such as *P. tenuirostris* are dolichocephalic.

The *Planigale maculata* group

This group comprises two species, *P. maculata* Gould and *P. novaeguineae* Tate and Archbold.

Planigale maculata (Gould) (Plates 43, 44, 51C–D)

Antechinus maculatus Gould, 1851, letterpress to pl. 44.
Antechinus minutissimus Gould, 1852, letterpress to pl. 45.

Phascogale minutissima sinualis Thomas, 1926, p. 634.
Planigale maculata Archer, 1975, p. 248.

TYPES

Antechinus maculatus Gould, 1851

HOLOTYPE: BM53.10.22.21, skin and skull, adult male, collected by J. Strange. The holotype has not been examined.

TYPE LOCALITY: Gould (1851, letterpress to plate 44) says '... was procured in the brushes near the river Clarence, a little to the southward of Moreton Bay.' Gould (1854, p. 284) says 'Brushes of the River Clarence, on the east coast of Australia.' Thomas (1888, p. 293) records the locality as 'Clarence R., Moreton Bay ...'. Tate (1947, p. 131) says the type specimen came '... from Clarence River, south of Moreton Bay, southern Queensland ...'.

Antechinus minutissimus Gould, 1852

HOLOTYPE: BM53.10.22.20, skin and BM54.10.21.5, skull, adult male, collected by J. Strange. The holotype has not been examined.

TYPE LOCALITY: Gould (1852, letterpress to plate 45) says '... habitat of the *A. minutissimus* is the districts on the eastern coast of Australia, in the neighbourhood of Moreton Bay.' Gould (1854, p. 285) says 'Hab. Brushes of the east coasts of Australia.' Thomas (1888, p. 293) gives 'Cressbrook, Moreton Bay ...'.

Phascogale minutissima sinualis Thomas, 1926

HOLOTYPE: BM26.3.11.194, skull and carcase in alcohol, juvenile male, obtained by Captain G. H. Wilkin's Expedition, 19 January 1925. The holotype has not been examined.

TYPE LOCALITY: Thomas (1926, p. 634) says 'Hab. Groote Eylandt, Gulf of Carpentaria.'

MATERIAL EXAMINED

Data sheets for specimens examined available in the library of the Queensland Museum.

Queensland: Mapoon Mission (AM M8149); Abergowrie (JM833); Coen (AM M8150); Wenlock (J8170); Mt Molloy (e.g. J16477); Mt Garnet (J7766); Herberton (J8244); East Funnell Creek above Sarina (AM M6983); Sarina (AM M6840); Yeppoon Crossing, Rockhampton (AM M8336); Rockhampton (J19668); Mt Larcom (J7002); Calliope (J8070); Biloela (J9856); Biggenden (J4374); Saunders Beach Rd, N. Townsville (Qd Museum); Upper Ross Store, Townsville (JM826); Major Creek, Woodstock (JM823); Lansdowne Stn, Woodstock (Qd Museum); Collinsville (WAM M6203); Coorgango Stn, nr Proserpine (J20256); Russell I, Moreton Bay (J10826); West Burleigh (J13171); Tamborine (J16685); Purga (e.g. J4105); Upper Brookfield, Brisbane (J13396); Maryborough (AM M662); Coogan Range, nr Yarraman (J13272); Aurukun Mission (e.g. C1483); Adel's Grove, Lawn Hill Ck (AM M5636).

New South Wales: 8 km W. Ballina (AM M8338); Bunnan, nr Scone (AM M7555); Boomi Creek, Urbenville (CSIRO no. CM492); Wallaby Knob, Tooloom (CSIRO no. CM233).

Northern Territory: Fogg Dam, Humpty Doo (e.g. WAM M8095); Darwin; Mataranka Homestead (AM M7382); King River (C7820); Katherine (AM M7043); Jim Jim Ck (W.A. Museum).

Western Australia: Drysdale River (W.A. Museum); Barrow Island (WAM M11020).

Distribution of specimens shown in Fig. 2.

DIAGNOSIS

Large species similar in size to *P. gilesi*, but differs from *P. gilesi* in possessing three premolars above and below and having non-reduced stylar cusp B. Differs from *P. novaeguineae* in smaller mean size and in several cranial ratios including

higher BW/ZW and BW/M^{1-3} which reflect relatively larger size of alisphenoid bullae. Differs from *P. ingrami* in being larger with non-flattened skull; larger M^2 stylar cusp D; relatively shorter supratragus of ear; greatly enlarged P^4 , almost twice P^1 crown height; non-reduced stylar cusp B; relatively conspicuous transverse canal foramen; paritals with relatively shorter, antero-dorsal extensions (horns); small condylar foramen; and several cranial ratios including large mean SD/IO and $PMX-NE/NL$ and smaller mean BL/M^{1-3} , FM/SD , and NW/NL . Differs from smaller *P. tenuirostris* in possessing relatively conspicuous transverse canal foramina, larger M^3 stylar cusp D, shorter head, and in lower BL/ZW ratio.

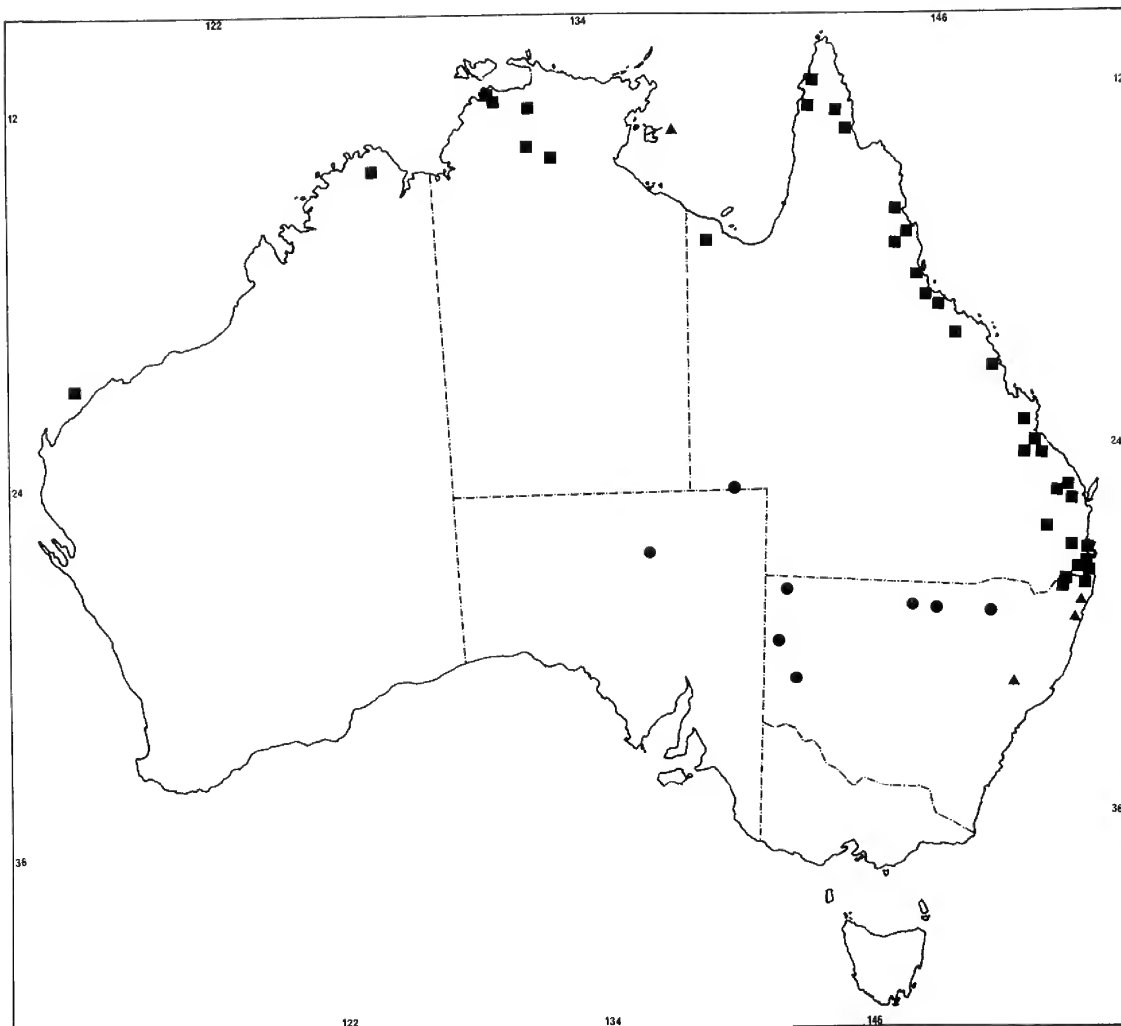


FIG. 2: Distribution of *Planigale maculata* (solid squares represent modern specimens examined; solid triangles represent literature records given by Marlow 1958 and Thomas 1926), and *P. gilesi* (solid dots represent modern specimens examined).

DESCRIPTION

Tail thin. Tail length variable being shorter than head-body length in typical form, longer in *sinualis* form, and, in general, relatively shorter than in other species. Davies (1960) lists external measurements for specimens of *sinualis* form from Humpty Doo, N.T. (as *P. ingrami*), which indicate mean TV/HB value of 0.90. This compares closely with series from Groote Eylandt described by Johnson (1964) with mean TV/HB value of 0.93. Type specimen of *sinualis* Thomas has TV/HB value of 0.90. Compared with this, typical *P. maculata* here examined have mean TV/HB value of 0.82.

Supratragus of ear longer in typical form than *sinualis* form, and relatively shorter than in most other species.

Nipple number varies from 5 to 10 (to possibly 15, Fleay 1967) in typical form, and 8 to 12 in *sinualis* form. Thomas (1888) records 8, Pocock (1926) records 6, Fleay (1965) records 7–9 (as *P. ingrami*, here regarded as including *P. maculata*, see below), for typical form and notes (1967) specimen with 15 young. In specimens of typical form examined here, two had 5 nipples (J21325, J8244), two had 6 (AM M6840, J2204), one had 7 (AM M662), one had 8 (J3345) and three had 10 (J21321, J19668, and J4374). From single locality, Mt Molloy, NE. Qd, J21325 had 5, and J21321 had 10. Davies (1960) records litters of 8 and 12 for animals from Humpty Doo, N.T., representing *sinualis* form. Aslin (1975) notes litters of 8, 10 and 11 for wild caught Humpty Doo animals. Johnson (1964) records 10 nipples for single specimen of *sinualis* form from Groote Eylandt. Specimen from Darwin has 10 nipples.

Pouch morphology varies in typical form, perhaps as function of reproductive stage. Juveniles held in captivity and examined live (5 August 1973) had poorly-developed, inconspicuous pouch. Adults, including live mother of juveniles noted above, had well-developed, deep pouch, but size and position of opening vary. Live adults appear to have ability to contract entrance to small, posteriorly positioned, circle. One individual examined (5 August 1973) had well-developed pouch which opened posteriorly, with walls on sides and 10 mm deep wall at anterior end. Some preserved adults (e.g. J21321 from Mt Molloy), apparently lactating, have pouches widely open postero-ventrally, presumably to accommodate larger young. Woolley (1974) comments on pouch morphology in *P. maculata*.

Mean IO/ZW ratio lower than in most other species, reflecting relatively restricted interorbital regions. Mean FM/ZW, and NW/NL ratios lower than in most other species. Mean

$(C^1-M^4)-(M^{1-4})/(M^{1-3})$ lower in typical than *sinualis* form and, in general, lower than in most other species. Mean SD/IO ratio higher in typical than *sinualis* form, reflecting less-flattened condition of typical skulls, and higher in this ratio than all other species except *P. novaeguineae*.

DISCUSSION

Although the holotypes of *Antechinus maculatus*, *Antechinus minutissimus* and *Phascogale minutissimus sinualis* have not been examined, topotypical material of *maculatus* and *minutissimus* has been examined. Consideration of this material, type descriptions, and descriptions given by Thomas (1888), Tate (1947), and Johnson (1964) leaves no doubt about the synonymy presented here. No topotypical specimens of *sinualis* have been examined. Few cranial measurements are given by Thomas (1926) and Johnson (1964) for *sinualis* but, where given, they closely correspond to measurements for Humpty Doo *Planigale* specimens.

Fleay (1965) records *P. ingrami* from Gin Gin, Gunalda, Numinbah Valley and Burleigh in SE.Qd. These records are apparently unsupported by museum specimens of *P. ingrami*. Several specimens (e.g. J13526 and J13171) collected by Mr Fleay from owl pellets at Burleigh, represent *P. maculata*. Fleay (1965) also reports *P. ingrami* from Monto, SE.Qd. The only museum specimen from Monto in the Queensland Museum (J15783) appears to represent *P. tenuirostris*. It is possible that the animals studied by Fleay may have represented both *P. maculata* and *P. tenuirostris*, although photographs, nipple counts and measurements given suggest only *P. maculata*.

Ride (1970) reports *P. maculata* from Western Australia. The specimen regarded by Ride (pers. comm.) to be *P. maculata* (WAM M3432) from Tambrey, Coolawanyah Station, may represent an undescribed taxon, and is discussed below (p. 357).

In general, *P. ingrami* and *P. maculata* are allopatric. The only instance of apparent sympatry between them occurs at Major Creek, Woodstock, NE.Qd (*P. maculata* JM823 and *P. ingrami* JM764). Marlow (1962) suggests they are also sympatric at Coen, NE.Qd. Examination of this material (AM M8148 and AM M8150) suggests both specimens represent *P. maculata*.

Specimens referred to *Planigale* by Van Deusen (1969) from northern Australia have not been examined. If *P. ingrami* occurs in areas of the Northern Territory other than the Barkly Tableland, it should be easy to distinguish this extremely flat-headed, tiny species from *P. maculata*.

FORMS OF *P. maculata*: There are at least two distinctive, allopatric forms of *P. maculata*. The typical form includes samples from Mt Molloy, Townsville, and other localities in eastern Queensland and northeastern New South Wales generally in and east of the Great Divide. A non-typical form occurs in northern Northern Territory, northwestern Queensland, Barrow Island and the Drysdale River area of Western Australia. No attempt has been made here to assess the possible statistical basis for recognizing subspecies. This non-typical form includes the type of *Phascogale minutissima sinualis* Thomas and the name *sinualis* is used here only as a convenient means of reference. This use is not to be interpreted as formal recognition of subspecific status. At present, too little information is available about *Planigale* from Cape York to determine the affinities of specimens from Aurukun Mission. They differ in several respects from *sinualis* and may represent a third form. Measurements of spirit carcasses provide a mean TV/HB value of 0.77, the lowest for any *maculata* series measured here. Shorter tails are recorded by other workers. Fleay (1965) reports two inch tails and three inch head and body measurements for male *P. maculata* (as *P. ingrami*) which gives a TV/HB ratio of 0.67. The mean ST/E value of the Aurukun Mission animals is very low and compares only with the mean figure for *P. tenuirostris*. Absolute size of almost all characters is smaller in Aurukun Mission specimens than in any other *maculata* measured. The only Aurukun female with a distinct pouch area appears to have nine very small nipples. It was evidently collected in August.

Although it is concluded here that the types of *maculatus* Gould and *sinualis* Thomas are conspecific, it is clear that they also represent different forms. The only major geographic barrier which appears to separate the allopatric ranges of these forms is the Gulf of Carpentaria. The Aurukun Mission population from the eastern edge of the Gulf of Carpentaria may be unique as a result of its isolation from the typical form by the inland areas of the Cape York Peninsula and from the *sinualis* form by the Gulf. It is probable that during the Plesitocene, with lowered sea levels, the Gulf of Carpentaria was not a significant barrier.

HABIT AND REPRODUCTION

Typical *maculata*: In N.S.W. they are rare and inhabit sclerophyll and rain-forest on the eastern side of the Great Divide (Marlow 1958). In Qd they are recorded from hollow logs and under sheets of iron, in timber country, flooded marsh, and rocky

areas (Fleay 1965); most specimens brought to the Queensland Museum from Brisbane area have been killed by cats; one was collected from a Cane Toad's stomach (Covacevich and Archer 1975).

In captivity they sometimes build saucer-shaped nests of dry grass or in deeper grass, more elaborate nests similar to those of Blue Wrens (Fleay 1965). Animals held by the author seemed opportunistic, building nests in hollow logs, between sheets of newspaper, and in boxes. As many as five individuals may nest together. Food preferred is insects but eggs, lean meat, chicken and honey are accepted. Small lizards and mammals are avoided. Movements in captivity indicate they are adept climbers, not hesitating to jump or drop distances of over 30 cm.

Fleay suggests from field observations and breeding in captivity that individuals of the typical form are summer breeders, earliest pouch development and pregnancy taking place in October and, if no pregnancy occurs, the pouch stops development by mid-January. Captive animals from Mt Molloy held by the author mated on 11 September 1973. This resulted in birth, but actual date of birth was not noted.

Sinualis form: At Humpty Doo, N.T., they occupy *Pandanus* and *Melaleuca* fringe areas bordering the Adelaide River flood plain (Davies 1960). In W.A. one individual was collected in hummock grass beneath *Acacia* on sandstone boulders in sand, on the edge of a tributary of the Drysdale River (Dr D. Kitchener, pers. comm.).

Aslin (1975) gives breeding data for this form in captivity, noting that it is polyoestrous with a gestation period of 19–20 days. Litters were born in February, March, April, July, September, October and December, single females having two or possibly more litters per year. Males were capable of breeding at least to 24 months in age. These observations are supported by the combined observations of Thomas (1926), Davies (1960), and Johnson (1964) which suggest this form is also polyoestrous in the field.

Planigale novaeguineae Tate and Archbold (Plate 45)

Planigale novaeguineae Tate and Archbold, 1941, pp. 7–8.

TYPE

HOLOTYPE: AMNH108561, skull and skin, adult male, collected by G. H. H. Tate, 20 January 1937. The holotype has not been examined.

TYPE LOCALITY: Tate and Archbold (1941, pp. 7–8) state: ' . . . Rona Falls, near Port Moresby, Central Division, Papua: 250 metres . . . '.

MATERIAL EXAMINED

Data sheets are available in the library of the Queensland Museum.

New Guinea: ♂, Waigani Swamp 16 km N. Port Moresby, coll. H. Cogger, 23 December 1963 (AM M9091); ♀, New Guinea, no other data (J4368).

DIAGNOSIS

Similar to *P. maculata* but differs in larger size; tendency for I^4 to exceed I^2 in crown length; several dental and cranial ratios including lower mean BW/ZW , BW/M^{1-3} , FM/SD , and higher mean SD/ZW and I_1-P_4/M_{1-3} ; and in variable tendency for tail to be longer than head and body. Differs from other species of *Planigale* by same features which distinguish *P. maculata*.

DESCRIPTION

Tail length variable, shorter than head and body in holotype and specimens noted by Ziegler (1972) but longer than head and body in J4368.

Hind foot, from description by Tate and Archbold (1941, p. 8), dried in holotype with 'Faint traces of striations on pads (rest of foot normally granulated as in *Antechinus* and other genera)'.

Nipple number unknown.

Mean BW/ZW and BW/M^{1-3} values lowest in *Planigale* reflecting very small alisphenoid bullae of *P. novaeguinae*. Mean SD/ZW value highest reflecting relatively deep skull of *P. novaeguinae*. Mean FM/SD value lowest indicating both narrow foramen magnum and relatively deep cranium. Mean $(I_1-M_4)-(M_{1-4})/M_{1-3}$ value highest.

DISCUSSION

The type specimen was previously the only specimen of *Planigale* recorded from New Guinea. Ziegler (1972) records three additional specimens, from Balimo, 450 km WNW. of the type locality. Two additional specimens were collected at Waigani Swamp, 16 km N. of Port Moresby, New Guinea, by Dr H. Cogger of the Australian Museum in 1963. Mr B. Marlow of the Australian Museum will describe these specimens elsewhere, but in the meantime has kindly allowed me to examine the skull of the adult male specimen, AM M9091. Menzies (1972) records numerous specimens of this species obtained from owl pellet material collected from the floor of a rock shelter near Mt Eriama, about 16 km from Port Moresby and 13 km from Rouna. A specimen in the Queensland Museum (J4368) identified on the label by Mr C. W. De Vis as coming from New Guinea, represents *Planigale*. The specimen is represented

by a skull, dentaries and dry, shrivelled and faded, carcase. A manuscript in De Vis' handwriting states that the fur is '... short and silky throughout ... mammae not apparent ... pads smooth of the three at the bases of the digits and the outermost has a small backward-curved prolongation; the plantar pad on the hallual side elongate and semi-divided, that on the outer side opposite and shorter ... above dark fawn, sides of muzzle distinctly darker but without a definite stripe; edges of eyelids nearly black, chin and throat nearly white passing into pale fawn on the rest of the lower surface, feet and tail brown above, paler brown below ... length of head and body 69 mm ...'. He expresses all other body measurements as percentages of the head-body length. Converting these values, the tail is 70.4 mm, the hind foot length (possibly including claws) 13.8 mm, hind foot breadth 3.0 mm, the ear (it is not apparent how it was measured and the figure seems small) 6.2 mm, the forearm and manus 11.0 mm. The habitat is stated to be 'New Guinea, locality unrecorded'.

Differences between J4368, and AM M9091 from Waigani Swamp, include the greater skull depth of AM M9091, 6.3, compared with 5.6 for J4368, indicating an SD/IO value of 1.34 for AM M9091 and 1.12 for J4368. Other differences are minor by comparison, and it is likely that these are sexual, AM M9091 being a male and J4368 a female. In other series, such as those of *P. maculata*, males almost invariably have deeper skulls and narrower interorbital values than females. Tate and Archbold's (1941) description of the type of *P. novaeguinae* indicates that although the skull was damaged in preparation, the braincase was, in their opinion, very flat. This specimen is a male, and therefore the degree of flattening may vary within, as well as between, sexes. Ziegler (1972) notes other possible sexual differences in *P. novaeguinae* from Balimo.

J4368 is smaller in many cranial and dental measurements than AM M9091. Measurements given by Tate and Archbold (1941) for the holotype are generally intermediate between these two. J4368 indicates that there is not as great a size difference between *P. novaeguinae* and other *Planigale* as the type specimen alone suggests. For example, AM M6893, male *P. maculata* from East Funnell Creek above Sarina, Queensland, is in most characters only just smaller than J4368 and in BL , ZW , OBW , $R-LM^3$, VV , $C-AP$, and $PLF-AB$ even exceeds J4368. Further, in some specimens (e.g. AM M6983 and AM M8336) of *P. maculata*, I^4 slightly exceeds I^2 in length, as in *P. novaeguinae*.

Tate and Archbold (1941, p. 8) describe the hind foot of the holotype as having 'Faint traces of striations . . . on the pads. Tate (1947, p. 134) says of this specimen that it is ' . . . the only one in which the foot pads are distinctly striated'. In alcohol specimens of *P. maculata* examined in the present study, most apical granules of the interdigital hallucal and metatarsal pads have visible striae without surface ridges. In some (e.g. C7428) the covering skin is thin on the apical granules and very low ridges appear present on the surface of the pad. In some alcoholic specimens of other species (e.g. AM M5021 *P. ingrami*) the apical granules are also striate with extremely low ridges on the pads. It has been noted in *Sminthopsis* (Archer, in preparation) that dehydration may emphasize striations by causing shrinkage of tissues over underlying sub-surface ridges. It is possible that the difference in opinion about the striate condition of the type specimen of *P. novaeguineae* given by Tate and Archbold (1941) and Tate (1947) may be the result of seven years of dehydration. In any case, the fact that other species sometimes have striated apical granules indicates that *P. novaeguineae* is not unique in this respect. It may, however, be a more common feature of specimens of that species.

HABITAT AND REPRODUCTION

The type specimen (Tate and Archbold 1941, p. 8) was caught on a ' . . . great rock-strewn slope . . . in a dryish place beneath an overhanging rock. The hillside was comparatively barren of vegetation . . .'. Ziegler (1972) notes that specimens caught at Balimo occurred in 'grass'. Menzies (1972, p. 404) notes that with the possible exception of a doubtfully identified juvenile *Pseudocheirus*, all of the species occurring with *P. novaeguineae* in the owl pellet material from near Port Moresby ' . . . are savanna dwellers. Closed forest lies within a few miles of the site and so well within the hunting range of a medium-sized bird but it is clear that it hunts only in the savanna.' He suggests that the relative abundance (6.5%) of the dasyurid material (over 90% of which was *Planigale*), may represent the abundance of these animals in the small mammal fauna of the Port Moresby savannas.

The *Planigale ingrami* group

This group comprises two species, *P. ingrami* (Thomas) and *P. tenuirostris* Troughton.

Planigale ingrami (Thomas) (Plates 46, 47, 51 A-B)

Phascogale ingrami Thomas, 1906a, pp. 541-2.

Phascogale subtilissima Lönnberg, 1913, pp. 9-10.
Planigale ingrami brunneus Troughton, 1928, pp. 282-5.

TYPES

Phascogale ingrami Thomas, 1906a

HOLOTYPE: BM6.3.9.77, skull and skin, adult male, collected by Mr W. Stalker, 30 April 1905. The holotype has not been examined.

TYPE LOCALITY: Thomas (1906b, p. 541-2) states 'Buchanan, Alexandria, 600' . . . central part of Northern South Australia'.

Phascogale subtilissima Lönnberg, 1913.

HOLOTYPE: Stockholm Museum no. 2482, skull and mounted skin, juvenile male, collected by the Swedish Scientific Expeditions, 2 February 1911. Photographs of skull have been examined.

TYPE LOCALITY: Lönnberg (1913, p. 9) says 'caught in crack of the earth on a plain near Noonkambah . . .'.

Planigale ingrami brunneus Troughton, 1928

HOLOTYPE: AM M2174, skull and carcase in alcohol, adult female, donated by Mr F. L. Berney. The holotype has been examined.

TYPE LOCALITY: Troughton (1928, p. 285) gives 'Wyangarie, on the Flinders River, Richmond district, northern Queensland.'

MATERIAL EXAMINED

Data sheets for specimens examined available in the library of the Queensland Museum.

Queensland: Richmond (e.g. J7655); Leslew Downs, nr Richmond (JM824); Alex Ck, approx. 8 km from Leslew Downs (JM763); Wyangerie, nr Richmond (AM M2174); Major Ck, nr Townsville (JM764); Red Falls, nr Lollworth Ck, 88 km NW. Charters Towers (Qd Museum); Charters Towers (Department Primary Industries, Townsville); Karumba, nr Normanton (e.g. AM M8468); Old Normanton (e.g. C3260).

Northern Territory: 200 km W. Burketown (e.g. AM M5022); owl pellets, Brunette Downs (N.T. Museum and noted in Parker 1973).

Western Australia: Ord River area (WAM M2846); Argyle Downs Stn (W.A. Museum); Wotjalum Mission, nr Derby (WAM M3191); cave surface, approx. 16 km SE. Fitzroy Crossing (e.g. 71.12.30); cave, Windjana Gorge (72.9.64); cave, between Kununurra and Ningbing Stn (JM827).

Distribution of specimens shown in Fig. 3.

DIAGNOSIS

Smallest species, also differing from other species in having tail commonly longer than head and body and in certain external, cranial, and dental ratios including highest mean BL/M¹⁻³ and NW/NL. Also differs from *P. maculata* and *P. novaeguineae* in lower mean SD/IO, PN/NL and higher mean FM/SD. Also differs from *P. tenuirostris* in lower mean SD/IO. Also differs from *P. gilesi* in having P4, and lower mean PN/NL.

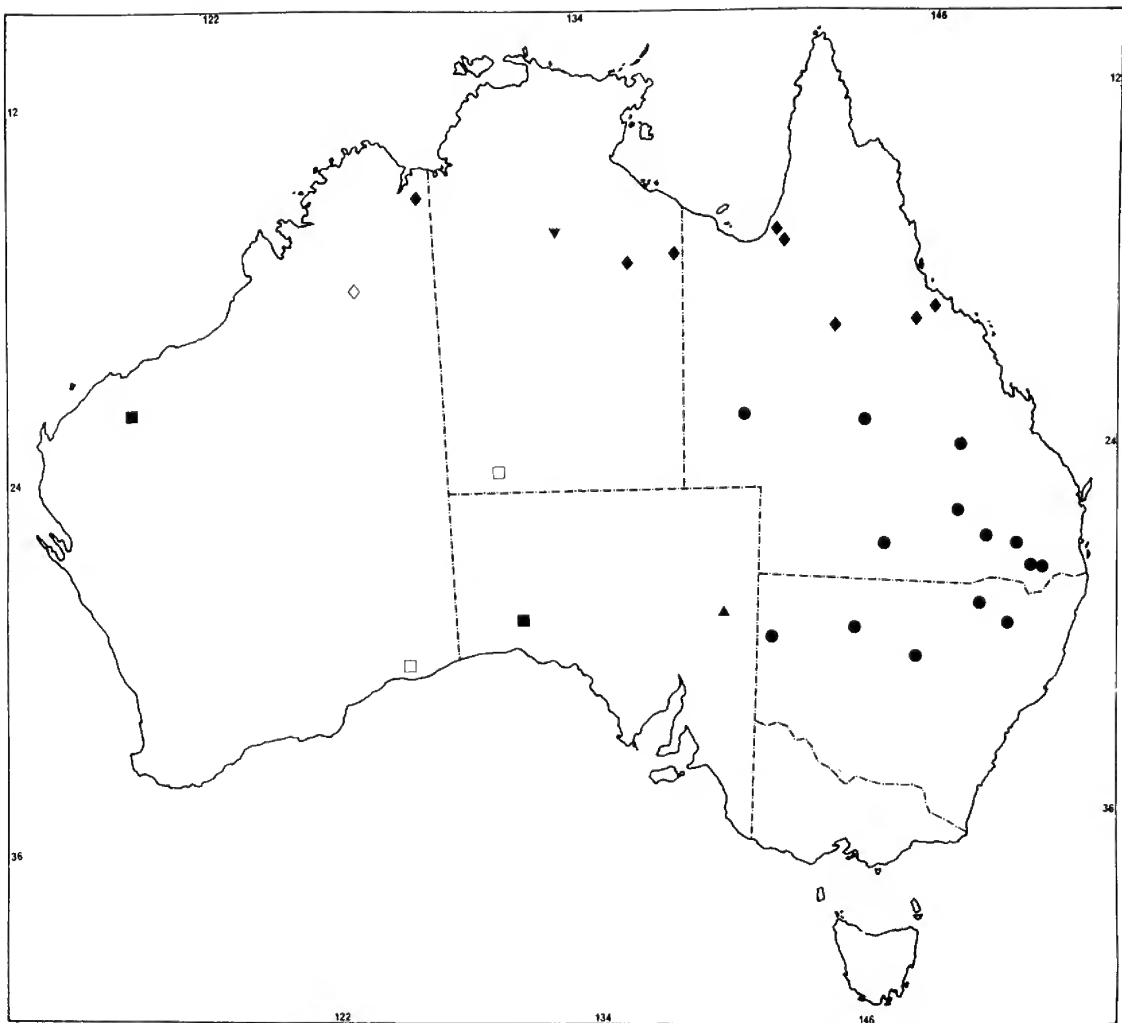


FIG. 3: Distribution of *Planigale ingrami* (solid diamonds represent modern specimens examined; hollow diamonds represent cave specimens examined; inverted solid triangle represents record given by Van Deusen 1969), *P. tenuirostris* (solid dots represent modern specimens examined; solid triangle represents record given by Aitken 1971), and *Planigale* sp. (solid squares represent specimens examined from Ooldea and Tambrey; hollow squares represent cave specimens from Ayers Rock and Madura).

DESCRIPTION

Tail invariably thin. Tail-vent length generally longer than head-body length, and longer in *subtilissima* than *brunneus* and typical forms. Thomas's (1906b) description of body measurements of lectotype and paratype of typical form, give mean TV/HB value of 0.75. Not clear from Thomas's description if all specimens (Thomas indicates five) collected by Stalker had shorter tails than head-body measurements. He states (p. 541) 'Tail of medium length . . . '.

Supratragus of ear relatively long, compared with other species and relatively longer in *subtilissima* than typical form.

Six to 10 nipples have been recorded. Heinsohn (1970) notes some individuals with 12 young. Three individuals of *subtilissima* form have 10 nipples, fourth appears to have only 9 and is presumably abnormal. Holotype *P. i. brunneus* has 6 nipples.

Pouch morphology may distinguish *subtilissima* from other forms (as suggested by Woolley 1974), although *subtilissima* form not unique in poss-

ession of accessory anterior pockets. Less well-developed pockets occur in *P. ingrami* from Richmond, and may occur in all forms but possibility cannot at present be checked. More detailed examination is required of possible changes in pouch morphology as a function of reproductive condition.

Thomas (1906b, p. 541) says of typical form 'General colour above not unlike that of paler wild-living forms of *Mus musculus*, something between Ridgway's "wood-brown" and "broccoli-brown", the hairs slaty grey, with pale tips . . . Under surface paler, with a yellowish tinge . . . the hairs slaty at base except on the chin. Crown like back. Cheeks and chin whitish. A whitish-buffy line just over each eye.' Two females of *subtilissima* form examined live are not identically coloured: one much darker than other with black nose; other noticeably lighter with caramel-coloured nose. This variation not clearly attributable to different habitats and may represent normal intra-specific variation. Heinsohn (1970) says of *P. ingrami* from near Townsville that individuals from areas of black basalt rock tend to be black, whereas those from non-basalt areas are grey or grey-brown. Individuals of *brunnea* form may be distinguished from typical form by brown basal fur.

Absolute size of many dental and cranial characters comparable with *P. tenuirostris*, smaller than *P. maculata*, *P. gilesi* and *P. novaeguineae*. Mean M_{1-3} length *P. ingrami* 3.1 compared with 3.0 for *P. tenuirostris*, 3.6 for *P. gilesi*, 3.6 for *P. maculata*, and 4.1 for *P. novaeguineae*. Various mean cranial ratio values distinctive as follows: mean SD/IO value comparable with that of *P. gilesi*, lower than that of *P. tenuirostris* and much lower than that of *P. maculata* and *P. novaeguineae*, indicating very flat head and broad interorbital region of *P. ingrami*; mean BL/M^{1-3} value *P. ingrami* higher than all other species, reflecting proportionately long periotic and alisphenoid bullae; mean FM/SD value comparable with *P. gilesi* and *P. tenuirostris* but considerably larger than *P. maculata* and *P. novaeguineae*; mean NW/NL value higher than that of any other species, indicating very short and wide (posteriorly) nasals of *P. ingrami*; mean PN/NL value comparable with that of *P. tenuirostris* but smaller than that of *P. gilesi*, *P. maculata*, and *P. novaeguineae*. Intraspecifically, *subtilissima* form generally distinguishable from typical form by relatively smaller P^4 . Difference in crown height between P^4 and P^1 noticeable, but less than two times height of P^1 . One individual (AM M5021) of typical form from 200 km W. Burketown similar, with only slightly enlarged P^4 . Both forms have well-developed posterior P^4 talon.

Specimens of *brunnea* form have highest mean FM/SD value of any *Planigale* population, reflecting relatively very flat heads and wide foramen magnum. This form also distinguished from *subtilissima* form by higher mean PMX-NAS/NL value and relatively longer lower premolar row. P^4 also relatively larger.

DISCUSSION

Cranial measurements given by Thomas (1906b) for *P. ingrami* are similar to those of specimens referred in the present study to *P. ingrami*. The very flat head and wide interorbital width values are very similar to those of specimens from Richmond and 200 km W. of Burketown. The SD/IO value of the lectotype, 0.87, is the same as that of the mean value for specimens from 200 km W. of Burketown and comparable with that of specimens of the *brunnea* form from Richmond. It is also comparable with the mean value for individuals of the *subtilissima* form. This feature, in conjunction with many other similar cranial and dental ratios and absolute measurements, indicates the general similarity of the type specimen to those of other samples regarded in this study as *p. ingrami*.

Heinsohn (1970) records several individuals of *P. ingrami* from the Townsville area. Examination of these specimens (including JM823 and JM764) indicates that *P. maculata* and *P. ingrami* are sympatric at Major Creek, Woodstock. Marlow (1962) records *P. ingrami* (AM M8148) from Coen, Queensland. This specimen has been examined and appears to be a juvenile *P. maculata*. Specimens referred by Fleay (1965, 1967) to *P. ingrami* probably represent *P. maculata* and possibly include some *P. tenuirostris*. Ride (1970) refers specimens from Laverton, Western Australia to *Planigale* cf. *P. ingrami* (plate 35). These specimens have been described as *Ningaui ridei* (Archer 1975). Ride (1970, p. 120) also refers to *P. ingrami* from ' . . . Kimberley and central W.A. . . .'. This material has been examined and, like all modern specimens of *Planigale ingrami* examined from the Kimberley region, appears to represent the *subtilissima* form of *P. ingrami*. One fossil sample from the southeastern edge of the Kimberley region is unusual (see below).

FORMS OF *P. ingrami*: There are at least two allopatric forms of *P. ingrami*. The typical form includes samples from the Barkly Tableland, in an area 200 km west of Burketown; and other areas in northeastern Queensland as far east as the Townsville area. The *subtilissima* form includes samples from the Kimberley Region. The *brunnea* form

includes samples from the Richmond area. Specimens from Old Normanton and Karumba, Queensland, are not clearly referable to any of these three and either represent a fourth form of *P. ingrami* or perhaps a mixed sample of more than one species. No attempt has been made here to assess the possible statistical basis for recognizing subspecies. Use of the formal names for these allopatric forms here is a matter of convenience and must not be interpreted as recognition of their subspecific status.

Lönnberg (1913) describes *Phascogale subtilissima* on the basis of a specimen that was shown by Tate (1947) to be juvenile. Tate considers the *subtilissima* form to be a race of *ingrami* and in this view is followed by Marlow (1968). Troughton (1928, 1967) and Ride (1970) regard it as a full species. Close similarity has been noted here between specimens of the *subtilissima* and typical forms. Although modern and fossil Kimberley specimens demonstrate morphological extremes, they are in most respects just one step beyond specimens from 200 km west of Burketown, which are also geographically closest to the Kimberley population. A cline may exist which links animals from the area west of Burketown, via the Barkly Tableland, to the Kimberley region. More specimens are required to test this possibility.

Fossil specimens (including 72.9.65 and 71.12.29–31) collected from surficial cave deposits in the southern Kimberley region, associated with a small mammal fauna which will be described elsewhere, represent at least nine individuals. They differ in some absolute measurements from specimens of the *subtilissima* form including mean I_1-M_4 length of the fossil specimens which is 5.9 mm as opposed to 6.7 mm for the *subtilissima* form. This results in a $(I_1-M_4)-(M_{1-4})/(M_{1-3})$ value of 0.83 for the fossil sample as opposed to 0.90 for the modern sample. This is also the lowest figure for any *Planigale* population. Further, mean length of the dentary of the fossil sample, 10.6 mm, is less than that of all other *Planigale*.

Troughton (1928) considers the *brunnea* form to differ from the typical form in possessing brown basal fur, longer tail, premaxillary vacuity which extends posteriorly to the middle of the C^1 alveolus, clear maxillary vacuity, P^1 barely two thirds of the height of P^3 rather than subequal, and broader nasals. Topotypical specimens J7655–6, give an idea of variation unavailable to Troughton. Both Queensland Museum specimens have premaxillary vacuities which extend beyond the level of the anterior edge of the C^1 . This is an almost universal condition in *P. ingrami* examined in the present study. It seems likely that the type of the species is

unusual in this respect (Thomas 1906b). Both Richmond specimens and all *Planigale* specimens examined have small, distinct maxillary fenestra, and this is not a useful diagnostic character for any subgeneric taxonomic rank. If these vacuities are not apparent, palatal skin has not been removed from the bony palate. Regarding premolar gradient, in J2655 P^3 is only slightly larger than P^1 and in J7656 P^3 is almost equal to P^1 in height. Regarding relative nasal breadth, the NW/NL value of the holotype of *brunneus*, using Troughton's (1928) measurements, is 0.49. This value for J7655 is also 0.49, while the measure for J7656 is 0.43. Regarding tail length, although measurements of J7655–6 are unknown, other samples serve to show that there is considerable variation in this character (see Table 2). This leaves basal fur colour as a possibly useful diagnostic character. This condition is indeterminable in J7655–6. However, Thomas (1906b) notes variation in fur colour. It therefore seems unlikely that the *brunnea* form is differentiable from the typical form using characters given by Troughton (1928), with the possible exception of basal fur colour.

Specimens from Old Normanton (C3259–60) and Karumba (AM M8467–9, M9144) are so variable that they may represent more than one species. Two specimens (both males) AM M8468 and AM M8469 from Karumba are more robust and broader-skulled than the third. AM M8467 (also male), from this locality. Specimens from Old Normanton (one male, one female) resemble in most respects AM M8467.

HABITAT AND REPRODUCTION

Typical ingrami: In N.T. they inhabit area around Alexandria draining inwards to Polygonum swamp (Thomas 1906b); at locality 200 km W. Burketown, they occur in tussocky grass, dry swamps and along perennial streams flowing out of the coastal ranges westward from Burketown (Troughton 1967); at New Castle Waters, one was found under bark near a small stream (Van Deusen 1969); generally not uncommon on black-soil plains, dry swamps and perennial watercourses of the Gulf drainage (Parker 1973). In Qd, 137 km SW. Townsville, one was found drinking from a rock pool (Heinsohn 1970).

In N.T., 200 km W. Burketown, they are said (Albert De Lestang, letter in Queensland Museum dated 8 October 1930) to breed in February to April, producing litters of 4 to 6 young. In NE.Qd they have litters of 4 to 12, reproduction occurring around December to March (Heinsohn 1970).

In captivity, an individual of the typical form constructed a series of covered runways and a hollow nest chamber in dry grass (Heinsohn 1970).

Subtilissima form: In W.A. they inhabit tussocks of grass near the Kimberley Research Stn and were also collected from piles of wet decomposing grass (Rudeforth 1950 and pers. comm.); on isolated hills on Argyle Downs Stn, while the waters of Lake Argyle were rising, they were collected from clumps of spinifex (Dr D. Kitchener and Mr W. H. Butler, pers. comm.).

One or two females from Argyle Downs Stn collected live in December–January 1971–2 had an unspecified number of young about 0.5 cm long in her pouch. A single juvenile was preserved before the mother was transported to Perth. She evidently consumed the remaining young in transit. During January, the other female's pouch underwent enlargement, elongation of pouch hairs and, towards the end of February, regression. No juveniles were born. Woolley (1974) notes changes in pouch morphology of these same individuals and concludes that this form breeds in summer months, unlike the majority of dasyurids.

Brunnea form: Habitat unknown. Holotype has pouch young but month of collection is not recorded.

Old Normanton: Habitat unknown. One specimen (AM M9144) with 8 (or possibly 9) nipples died June 1965. The pouch was developing but clearly not in breeding condition.

Planigale tenuirostris Troughton (Plate 48)

Planigale tenuirostris Troughton, 1928, pp. 285–7.

TYPE

HOLOTYPE: AM M3933, skull and carcase in alcohol, adult female, collected by R. Helms in May or June 1890. The holotype has been examined.

TYPE LOCALITY: Troughton (1928, p. 287) says 'Collected at Bourke or Wilcannia, New South Wales, during the Darling River floods.'

MATERIAL EXAMINED

Data sheets for specimens examined available in the library of the Queensland Museum.

Queensland: Cunnamulla (AM M6957); Warwick (J7559); Pittsworth (J3096); Roma (J3824); 16 km NE. Longreach (J17549); Glenmorgan (J10109); Belmont, via Rockhampton (J14089).

New South Wales: Bourke or Wilcannia, Darling River (AM M3933); Bellata (AM M6879); Cullubri, 43 km SSE. Nyngan (AM M8151); Fowlers Gap (e.g. JM831).

Distribution of specimens shown in Fig. 3.

DIAGNOSIS

Small, very similar to *P. ingrami* but differs in relatively shorter supratragus of ear; tail being generally shorter than head-body length; and in several cranial ratios including lower mean BL/M¹⁻³ and NW/NL, BW/M¹⁻³, BL/M¹⁻³ and higher mean SD/IO, SD/ZW, and BL/ZW. Differs from *P. novaeguineae* and *P. maculata* in being smaller; in having relatively reduced transverse canal foramina; smaller styler cusp D on M³; longer head; wider interorbital distance; and in several cranial ratios including lower mean BL/ZW, PN/NL, SD/IO and higher mean NW/ZW, BL/ZW, BL/M¹⁻³, FM/SD, and FM/ZW. Differs from *P. gilesi* in having P4.

DESCRIPTION

Mean TV/HV value, 0.87, indicates relatively short-tailed condition.

Mean ST/E value, 0.28, lowest of any *Planigale* except *P. maculata* from Aurukun Mission. Mean absolute supratragus length, 2.6 mm, shortest.

Troughton (1928) notes holotype has 11 nipples but suggests normal number is 10. J7559 from Warwick, Queensland, has 7. J3096 from Pittsworth, Queensland, has 8.

Mean BL/ZW value highest indicating relative dolichocephaly. Mean NW/NL value lower than any *P. ingrami*, demonstrating relatively narrow nasals. Other differences indicated in Tables 1–2.

DISCUSSION

Troughton (1928) describes characters which he believes are useful in diagnosing *P. tenuirostris*. Having examined larger series of specimens of *P. ingrami* than were available to Troughton, it is clear that some of these characters are also variably present in *P. ingrami*. For example, Troughton (1928) says *P. tenuirostris* has 10 or 12 nipples in contrast to *P. ingrami* which has 6. As noted above, the *subtilissima* form may have 10 nipples, the typical form of *P. ingrami* from 200 km west of Burketown may have 10, the typical form of *P. ingrami* from near Townsville (Heinsohn 1970) may have 6 to 12, *P. gilesi* has 12 (Aitken 1972), and some *P. maculata* may have 8 to 15 (Fleay 1965, 1967, Davies 1960). Troughton (1928) considers that *P. tenuirostris* has more elongate premaxillae than *P. ingrami*. In some cases, this appears to be true. However, mean premaxilla-nasal contact length, a measure of this character, is 2.4 mm in specimens of *P. tenuirostris*, and 2.3 mm in specimens of *P. ingrami* from near Richmond, indicating little, if any, difference. Troughton (1928) describes P¹ as being two-thirds the size of

P³ in *P. tenuirostris* and subequal in typical *P. ingrami* (Thomas 1906). This character appears variable in *P. ingrami* (see above) and *P. tenuirostris*. Troughton (1928) considers *P. tenuirostris* to differ from the *brunnea* form of *P. ingrami* in its narrower hind foot, a condition which may relate to some circumstance of death. Among specimens of *P. ingrami*, AM M5022 has a hind foot noticeably wider distally than AM M4744 from the same locality. The widely spread foot of AM M5022 suggests the animal may have died and been fixed in muscular spasm. Finally, Troughton (1928) considers *P. tenuirostris* to differ from the *brunnea* form of *P. ingrami* in possessing a posterior notch on the lower part of the pinna of the ear. On the basis of larger series, this appears variable in both *P. tenuirostris* (e.g. slight or absent in AM M7313 and pronounced in holotype) and *P. ingrami* (small notch present in AM M5022 but not present in holotype of *P. i. brunneus*).

Van Deusen (in Fleay 1965) suggests *P. tenuirostris* may be a race of *P. ingrami*. The evidence seems inadequate to decide one way or the other. The present study only suggests that specimens referred here to *P. tenuirostris* exhibit some extremes in size and proportion, and most appear to inhabit more central or arid areas.

Marlow (1958) refers some specimens (AM M7033, M7393, M7819 and M7820) to this species from New South Wales. Aitken (1971) refers these to *P. gilesi*.

HABITAT AND REPRODUCTION

Aitken (1972) notes *P. tenuirostris* (AM M6879 and AM M7313) is sympatric with *P. gilesi* (AM M7033) from Bellata, New South Wales, and that (1971) a dehydrated specimen of *P. tenuirostris* (SAM M8405) was found at the bottom of a disused stone tank at Mulga Creek Well, near the northeastern tip of the Flinders Range, South Australia. In the same tank was a specimen of *Sminthopsis crassicaudata*.

Troughton (1928) notes the holotype, collected during the Darling River floods in May or June, 1890, has a well-developed pouch with enlarged nipples.

HOLOTYPE

The holotype has been examined. Troughton (1928, fig. 2) illustrates the ear, nose, hind foot, and skull of the holotype. Specimen numbers given by Troughton appear to be confused. The holotype is stated to be AM M3856, but AM M3933 in the Australian Museum is labelled as the holotype. AM M3856 is (pers. comm. Mr B. Marlow, 1975)

listed in the Australian Museum catalogue as *Pteropus poliocephalus* from Tamborine, south Queensland.

The *Planigale gilesi* group

This group contains only *P. gilesi* Aitken.

Planigale gilesi Aitken (Plate 49)

Planigale gilesi Aitken, 1972, pp. 1–14.

TYPE

HOLOTYPE: SAM M8046, dry skin and skull, torso in spirit, adult male, collected by messrs P. Aitken, A. Kowanko, J. Forrest and J. Howard, 29 June 1969. The holotype has been examined.

TYPE LOCALITY: Aitken (1972, p. 1) gives 'No. 3 Bore, Pastoral Property of Anna Creek, South Australia (lat. 28° 18'S, long. 136° 29' 40"E).'

MATERIAL EXAMINED

Data sheets for specimens examined available in the library of the Queensland Museum.

Queensland: Durrie Stn, 97 km E. Birdsville (J21973).

South Australia: Anna Creek (e.g. SAM M8406).

New South Wales: Bellata (e.g. AM M7033); Brewarrina (e.g. AM M7819); Fowlers Gap; Mt King, 27 km N. Tibooburra (AM M9829).

Distribution of specimens shown in Fig. 2.

DIAGNOSIS

Large species of *Planigale* differing from all others by having only two upper and lower premolars on each side as adult condition.

DESCRIPTION

Tail thin to slightly incrassated. Shorter than head and body length. Mean TV/HB value 0.96.

Supratragus of ear relatively long. Mean ST/E value 0.36.

Apical granules of interdigital pads of hindfoot have striae which do not reflect incident light and hence do not occur as ridges on surface of granule.

Aitken (1972) records twelve nipples.

Cranium wide and very flat. Parietal horns extend anteriorly to level near anterior end of cerebral hemispheres. Mean SD/IO value, SD/C¹ – M⁴ and several other cranial and dental ratios (see Table 2) very similar to those of otherwise smaller *P. ingrami*.

DISCUSSION

P. gilesi is the most distinctive species of the genus because of the reduced premolar number. When premolar reduction or loss occurs in other

dasyurids (e.g. some *Antechinus*, *Neophascogale* Stein, 1933, *Phascosorex* Matschie, 1916, *Myoictis* Gray, 1858, *Dasyercus*, *Dasyuroides*, *Dasyurus* Matschie, 1916) invariably the posterior premolar is reduced. This predisposition to reduce or lose P₄ in dasyurids has previously been noted (e.g. Thomas 1887, Bensley 1903, Tate 1947). In genera in which only some species have lost premolars, others show reduction of P₄. For example, all *Antechinus rosamondae* Ride, 1964 have two premolars above and below. Some individuals of *A. macdonnellensis* (Spencer, 1896) show the same condition. Others show a small P₄ above and below. Still others lack P₄ altogether. There is therefore a structural gradient of loss within the genus. In *Planigale*, two trends in premolar size are evident. In all species P₁ and P₁¹ are reduced, possibly the result of the very large canines, and (except in *P. gilesi*) P₄ is markedly reduced while P₄¹ is grossly enlarged into a tall shearing blade. Only the *subtilissima* form of *P. ingrami* does not show gross enlargement of P₄¹, but even here, P₄¹ is larger than P₃. If these trends in *Planigale* are used to interpret tooth loss in *P. gilesi*, the most logical conclusion is that P₁¹ and P₄ have been lost. If this were so, the anterior upper premolar (P₃) should shear behind the posterior lower premolar (P₃), a situation which does not exist. If P₁¹ and P₄ were lost, there must have been an intermediate stage in which premolars did not occlude in order that the anterior upper premolar and posterior lower premolar could bypass one another. Such an intermediate stage of non-occlusion is improbable and it is concluded that *P. gilesi*, like all other dasyurids which exhibit premolar reduction, has lost P₄¹ and P₄.

Loss of P₄¹ and P₄ in *P. gilesi*, in spite of the trend for reduction of P₁¹ rather than P₄¹ in other *Planigale*, indicates the magnitude of the structural gap between *P. gilesi* and other *Planigale*.

HABITAT AND REPRODUCTION

Aitken (1972) describes the habitat as bullrush and sedge plant associations developed around a bore drain in an area where average annual rainfall is less than 125 mm per year. Other sympatric species include *Canis familiaris*, *Sminthopsis froggatti*, *Pseudomys desertor*, *Rattus villosissimus*, *Mus musculus*, and introduced mammals such as rabbits, foxes, cats, camels, horses and cows. Aitken (1972) concludes *P. gilesi* is at least partially insectivorous.

None of the specimens examined by Aitken (1972) indicate the breeding season. Of two females with undeveloped pouches, AM M7033 (according

to the label) was collected in June (Aitken says 27 Feb.) and SAM M8411 was collected in August.

HOLOTYPE: The holotype has been examined. The skull and dentary are figured by Aitken (1972, plate 3).

Planigale, incertae sedis

Two specimens of *Planigale* examined in this study are not clearly referable to any described species. Both are damaged, and until better material comes to hand, they should not be named. A third form is described by Lundelius and Turnbull (1973).

J16732

A juvenile collected by A. S. Le Souef from Ooldea, Transcontinental Railway, South Australia (Fig. 3). Because it is juvenile (P₄ has not completely erupted), most cranial and dental measures cannot be meaningfully compared with those of adults of other species. It is most similar to *P. tenuirostris*. The bullae appear to be very much smaller than those of *P. tenuirostris*. P₄ (excavated) is 0.45 mm long; P₃ is 0.70 mm long; P₁ is 0.60 mm long.

WAM M3432 (Plate 50)

This specimen, the basis of Ride's (1970, p. 120) recognition of *Planigale maculata* in Western Australia, consists of a broken skull and somewhat damaged skin of an old adult male, collected by Mr W. H. Butler on 3 August 1958, from Tambrey, Coolawanyah Station, Hammersley District of Western Australia (Fig. 3). P₄ is double-rooted, a very unusual condition in *Planigale*. M¹⁻³/ZW value, 0.32, is lower than the mean of any other *Planigale* population. (C¹ - M⁴) - (M¹⁻⁴)/M¹⁻³ value, 0.82, is larger than the mean for any other *Planigale* population. This specimen may represent an unnamed species of *Planigale* but the specimen is too incomplete and isolated to permit adequate comparisons. P₄ is 0.56 mm long; P₃ 0.65 mm long; and P₁ 0.60 mm long.

THE MADURA FORM

Lundelius and Turnbull (1973) describe a Quaternary *Planigale* from Madura Cave, on the Roe Plain of the Western Australian Nullarbor (Fig. 3). After comparing it with several specimens of *P. ingrami* and one specimen of *P. maculata*, they conclude (p. 27) '... the Madura Cave material cannot be referred to any of the described species of pygmy antechinuses', and consider (p. 18) it is similar to *P. maculata* in having P₁ crowded out of

alignment in the tooth row, a feature which contrasts with *P. ingrami*. An examination of larger series of specimens than those available to Lundelius and Turnbull suggest this character is variable in *P. ingrami* and *P. maculata*. Two out of 5 modern *P. ingrami* have P¹ crowded out of alignment (e.g. J7656) and 1 (J17549) has LP¹ crowded out of line while RP¹ is straight. In 2 other specimens, P¹ is straight on both sides. In 10 *P. maculata* (a single sample from Mt Molloy), 3 specimens (e.g. J16730) have P¹ crown straight, 5 (e.g. J16481) have the crown slightly crowded out of alignment, and 2 (e.g. J16729) have the crown markedly crowded out of alignment. In *P. tenuirostris* all 4 specimens examined have the P¹ crown straight, as does the single specimen of *P. gilesi* checked for this character. Lundelius and Turnbull also suggest (p. 20) that the Madura *Planigale* resembles *P. maculata* in having a less-indented ectoloph immediately anterior to stylar cusp D (their mesostyle) than is present in *P. ingrami*. An examination of this character in 10 *P. ingrami* and 10 *P. maculata* similarly suggests the character is not constant in either of the two modern species. In J15891, the ectoloph is as deeply indented as in most *P. ingrami* and more deeply indented than others. It reveals that stylar cusp D is in general larger in *P. maculata* than *P. ingrami* and in this respect the Madura *Planigale* more closely resembles the latter. Lundelius and Turnbull also note (p. 22) that in the Madura *Planigale*, P₄ is generally straight while P₁ is crowded out of alignment, and in this respect it is unlike *P. ingrami*. In a series of modern *P. ingrami* examined in this study, orientation of P₄ appears to be variable. In J17549, P₄ is straight while P₃ and P₁ are slightly crowded out of alignment. In J7656 and J7655, P₄ is crowded out of alignment. In *P. maculata*, some specimens have P₄ straight (e.g. J16477, J16730), slightly turned (e.g. J16729, J16481), or markedly turned (e.g. J16482, J15891). Similar variation occurs in *P. tenuirostris*. The Madura *Planigale* is very distinctive in regard to the large size of P₄, as noted by Lundelius and Turnbull. No P₄ of any modern *Planigale* examined in the present study is of comparable length, not even the two-rooted P₄ of WAM M3432.

SUMMARY OF RESEMBLANCE WITHIN *Planigale*

Typical *P. maculata* and *P. novaeguineae* are very similar, and may prove conspecific. A general trend of increasing size exists in coastal populations north from New South Wales into New Guinea. Other trends such as reduction in size of alisphenoid bullae are also demonstrated. *P. nova-*

eguineae appears, in most respects, to represent no more than one end of this cline. Northern Territory and northwestern Queensland *P. maculata* (possibly all referable to *P. m. sinuialis*) are distinct from the typical form.

P. ingrami and *P. tenuirostris* are similar and it is not clear that they are separate species. These two forms are similar to *P. gilesi*, which because of premolar loss involving a reversal of a trend developed in the remaining species of the genus, is otherwise very distinct from all other *Planigale*.

The *subtilissima* form of *P. ingrami* is distinctive, while the *brunnea* form may be identical with the typical form of *P. ingrami*.

There may be additional undescribed forms of *Planigale* represented by single specimens or small samples, at present too inadequate to assess taxonomically.

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APPENDIX

Since this paper went to press I have had an opportunity to examine specimens of *Planigale* in the United States and England, and can make the following comments.

Specimens in the collections of the American Museum of Natural History include:

P. maculata (AMNH 160075-6, near Townsville, Qd. AMNH 193959, Gunalda, N. of Gympie, Qd. AMNH 160374, Monto, Qd. AMNH 18380, the *sinualis* form, Red Bank Mine, 18 miles (29 km) W. Wollongarang, N.T.). AMNH 193959 and 160374 were donated by Mr D. Fleay and support the suggestion made above that at least some of the specimens reported by Fleay (1965) represent *P. maculata* rather than *P. ingrami*.

P. novaeguineae (AMNH 108561, Holotype, Rona Falls, nr Port Moresby, Papua: measurements: C¹-M⁴, 8.2; M¹⁻⁴, 4.9; M¹⁻³, 4.3; I₁-M₄, 9.5; M₁₋₄, 5.3; M₁₋₃, 4.0; nasal length, 9.2; maximum width of nasals, 4.0; minimum width of nasals, 1.7; pmx-nasal suture, 4.1; the skull is badly smashed and lacks RI₁₋₃, RP₁, RP₄, LI₁-P₄, and RM²⁻⁴; foot pads are faintly striated, clearly the result of dehydration).

P. ingrami (AMNH 160313, Karumba, Qd. appears to represent this species but I have not examined the skull so reference here is tentative).

Specimens in the collections of the British Museum (Natural History) include:

P. maculata (BM53.10.22.21, Holotype, Clarence R., Moreton Bay, Qd: measurements: C¹-M⁴, 6.7; M¹⁻⁴, 4.0; M¹⁻³, 3.7; R-LM³, 6.2; IPVD, 4.5; I₁-M₄, 7.3; M₁₋₄, 4.6; M₁₋₃, 3.4; nasal length, 6.8; minimum width of nasals, 0.8; pmx-nasal suture, 2.9; the skull is only represented by a rostrum with damaged lower jaws, and lacks RP₁ and LP₁. Skin with number 53.10.22.21. is type and has locality as Clarence R., Moreton Bay; vague white spots are apparent on ventral side and flanks; it has damaged feet and scrotal area. BM54.10.21.5, Holotype

of *minutissima*, Cressbrook, N.S.W.: measurements: ZW, 10.5; C¹-M⁴, 6.8; M¹⁻⁴, 4.2; M¹⁻³, 3.8; R-LM³, 6.4; IO, 4.1; IPVD, 4.4; DL, 13.5; I₁-M₄, 7.7; M₁₋₄, 4.4; M₁₋₃, 3.4; C-AP, 4.0; C-AR, 4.4; SD, 5.3; nasal length, 7.1; maximum nasal width, 3.2; minimum nasal width, 1.2; pmx-nasal suture, 2.5; the rear of skull is badly damaged. Skin with number 53.10.22.20, is type and has locality as Cressbrook, Moreton Bay; it has damaged feet and ventral surface; BM26.3.11.194, Holotype of *sinualis*, Groote Eylandt: measurements of this juvenile with M³ erupting were not made except for M₁₋₃ which is 3.7; skin is in good condition. BM76.3.29.2, Peak Downs, Qd. BM91.6.28.1, N.S.W. BM25.8.1.133, locality?. BM75.14.1.23.5-6, Gin Gin, Qd).

P. novaeguineae (BM 73.145, Mt Eriama, about 10 miles (16 km) from Port Moresby and 8 miles (13 km) from Rouna, Papua).

P. ingrami (BM6.3.9.77, Holotype, Buchanan, Alexandria, N.T.: measurements: BL, 17.0; ZW, 9.4; OBW, 7.2; IBW, 2.3; C¹-M⁴, 6.0; M¹⁻⁴, 3.5; M¹⁻³, 3.1; R-LM³, 5.7; IO, 3.9; IPVD, 3.9; DL, 12.9; I₁-M₄, 6.8; M₁₋₄, 3.9; M₁₋₃, 3.0; C-AP, 3.7; C-AR, 3.7; SD, 3.6; bullar length, 4.9; nasal length, 6.7; maximum nasal width, 2.8; minimum nasal width, 1.0; pmx-nasal suture, 2.5; FM, 3.7; skull represents very old individual with worn teeth and lacks RM² although loss occurred during life; skin is in good condition. BM6.3.9.76, BM6.3.9.78, Buchanan, Alexandria, N.T.. BM6.3.9.79, Bluff Hole, Alexandria, N.T.. BM6.3.9.80, Alexandria, N.T.. BM25.4.9.8, the *subtilissima* form, Derby, W.A.).

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Abbreviations: BL, basicranial length; ZW, zygomatic width; OBW, outside bullar width; IBW, inside bullar width; FM, maximum width foramen magnum; IO, minimum interorbital width; VV, inter-palatal vacuity distance; DL, dentary length; C-AP, articular condyle to anterior border of ascending ramus; C-AR, articular condyle to tip of angular process; NL, nasal length; NW, maximum nasal width; NWMN, minimum nasal width; PN, nasal-premaxillary suture length; PLF-AB, bullar length from posterior lacerate foramen to anterior end alisphenoid tympanic wing; SD, skull depth; N, number of specimens in sample; $\bar{x} \pm \tau$, sample mean \pm one standard error; O.R., observed range; s, standard deviation; CV, coefficient of variation.

TABLE 1: ABSOLUTE MEASUREMENTS IN SPECIES OF *Planigale*

	N	$\bar{x} \pm \tau$	OR	s	CV		N	$\bar{x} \pm \tau$	OR	s	CV
	Planigale novaguineae						P. maculata (total)				
BL	2	21.4+.98	20.0-22.7	1.38	6.46	38	18.3+.14	16.4-20.2	0.86	4.67	
ZW	2	12.3+.75	11.5-13.1	1.06	8.64	40	10.6+.10	9.3-12.0	0.66	6.24	
OBW	2	8.1+.57	7.6- 8.5	0.80	9.88	40	7.3+.07	6.7- 8.3	0.41	5.68	
IBW	2	3.2+.46	2.9- 3.5	0.65	20.35	38	2.6+.04	2.1- 3.1	0.25	9.60	
C ¹ -M ⁴	2	8.3+.50	7.9- 8.6	0.70	8.52	43	6.9+.05	6.4- 7.6	0.31	4.49	
M ¹ - ⁴	2	4.8+.33	4.6- 4.9	0.47	9.84	44	4.3+.02	4.0- 4.6	0.15	3.47	
M ¹ - ³	2	4.3+.27	4.2- 4.4	0.38	8.73	48	3.9+.02	3.7- 4.2	0.13	3.29	
R-LM ³	2	7.2+.46	6.9- 7.5	0.65	9.04	41	6.4+.04	5.8- 7.1	0.29	4.46	
FM	2	4.3+.38	4.1- 4.5	0.53	12.35	37	4.0+.04	3.5- 4.2	0.25	6.02	
IO	2	4.9+.33	4.7- 5.0	0.47	9.64	42	4.2+.04	3.8- 4.8	0.24	5.72	
VV	2	5.6+.75	4.8- 6.4	1.06	18.98	42	4.5+.06	3.6- 5.3	0.38	8.46	
DL	2	16.6+.78	15.7-17.4	1.10	6.61	45	14.0+.13	12.6-15.7	0.84	5.99	
I ₁ -M ₄	2	9.6+.53	9.2-10.0	0.75	7.83	44	8.1+.06	7.5- 8.9	0.37	4.54	
M ₁ - ₄	2	5.4+.33	5.2- 5.5	0.47	8.74	44	4.7+.02	4.4- 5.0	0.16	3.33	
M ₁ - ₃	2	4.1+.33	3.9- 4.2	0.47	11.52	46	3.6+.02	3.3- 3.9	0.16	4.57	
C-AP	2	4.7+.33	4.5- 4.8	0.47	10.05	42	4.1+.04	3.7- 4.6	0.23	5.62	
C-AR	2	5.0+.53	4.6- 5.4	0.75	15.03	42	4.2+.04	3.5- 4.7	0.29	6.83	
NL	2	9.0+.65	8.4- 9.6	0.92	10.32	40	7.4+.09	6.4- 8.4	0.54	7.29	
NW	2	3.8+.27	3.7- 3.9	0.38	9.88	41	2.9+.04	2.3- 3.5	0.28	9.49	
NWMN	2	1.6+.22	1.5- 1.6	0.32	19.76	40	1.3+.02	1.1- 1.6	0.13	10.38	
PN	2	3.5+.35	2.9- 4.0	0.50	14.17	39	3.0+.06	2.3- 3.6	0.37	12.30	
PLF-AB	2	4.7+.22	4.6- 4.7	0.32	6.73	37	4.4+.04	3.8- 4.8	0.22	4.99	
SD	2	6.0+.50	5.6- 6.3	0.71	11.79	41	4.8+.04	4.2- 5.4	0.29	5.96	
	P. m.(Qld)						P. m.(Mt Molloy)				
BL	23	18.3+.19	16.9-20.2	0.91	4.99	7	18.9+.35	18.0-20.0	0.94	4.97	
ZW	24	10.6+.134	9.3-12.0	0.70	6.57	7	11.1+.22	10.2-11.9	0.57	5.16	
OBW	24	7.2+.115	6.7- 8.3	0.41	5.65	6	7.4+.14	7.0- 7.8	0.33	4.51	
IBW	22	2.6+.175	2.2- 3.0	0.21	8.22	6	2.6+.10	2.3- 3.0	0.25	9.69	
C ¹ -M ⁴	26	6.9+.104	6.5- 7.4	0.30	4.28	7	7.2+.06	7.0- 7.4	0.16	2.24	
M ¹ - ⁴	27	4.3+.68	4.0- 4.6	0.15	3.60	7	4.4+.04	4.3- 4.6	0.11	2.45	
M ¹ - ³	31	3.9+.61	3.7- 4.2	0.13	3.28	9	4.0+.03	3.9- 4.1	0.08	1.98	
R-LM ³	25	6.4+.95	5.9- 7.1	0.30	4.75	7	6.6+.07	6.4- 6.9	0.19	2.83	
FM	22	3.9+.93	3.5- 4.2	0.17	4.36	7	3.9+.08	3.6- 4.2	0.20	5.13	
IO	25	4.3+.114	4.0- 4.8	0.24	5.70	7	4.5+.06	4.3- 4.8	0.16	3.58	
VV	26	4.5+.204	3.6- 5.3	0.38	8.37	7	4.6+.13	4.3- 5.3	0.35	7.52	
DL	28	13.9+.149	12.6-15.7	0.85	6.10	7	14.5+.25	13.5-15.5	0.66	4.53	
I ₁ -M ₄	27	8.1+.89	7.5- 8.8	0.38	4.64	7	8.4+.05	8.3- 8.6	0.14	1.68	
M ₁ - ₄	28	4.7+.59	4.4- 4.9	0.15	3.14	7	4.8+.02	4.8- 4.9	0.04	8.33	
M ₁ - ₃	31	3.6+.81	3.4- 3.9	0.16	4.50	9	3.7+.03	3.6- 3.8	0.09	2.34	
C-AP	26	4.1+.157	3.7- 4.6	0.26	6.43	6	4.4+.06	4.2- 4.5	0.15	3.36	
C-AR	26	4.1+.179	3.5- 4.7	0.30	7.35	6	4.2+.12	2.9- 4.7	0.31	7.12	
NL	25	7.4+.148	6.5- 8.3	0.55	7.38	7	7.9+.12	7.4- 8.3	0.31	3.97	
NW	25	2.9+.172	2.5- 3.4	0.25	8.58	7	2.9+.06	2.6- 3.0	0.15	5.21	
NWMN	25	1.3+.222	1.1- 1.6	0.14	11.09	7	1.2+.05	1.1- 1.5	0.14	11.75	
PN	25	3.0+.234	2.3- 3.6	0.35	11.72	7	3.3+.13	2.8- 3.6	0.35	10.73	
PLF-AB	22	4.3+.100	4.0- 4.8	0.20	4.67	7	4.4+.03	4.4- 4.6	0.09	2.07	
SD	24	4.9+.105	4.4- 3.4	0.25	5.16	7	5.0+.07	5.9- 5.4	0.18	3.62	
	P. m. (Townsville)						P. m.(sinualis form,N.T.)				
BL	2	18.7+.57	18.2-19.1	0.80	4.28	10	18.5+.06	17.6-19.9	0.20	1.10	
ZW	2	10.9+.27	10.8-11.0	0.38	3.45	11	10.8+.12	10.1-11.4	0.39	3.57	
OBW	2	7.4+.22	7.0- 7.8	0.33	4.51	11	7.6+.09	7.1- 8.0	0.30	3.95	
IBW	2	2.8+.22	2.7- 2.8	0.32	11.29	11	2.8+.06	2.3- 3.1	0.21	7.46	
C ¹ -M ⁴	2	6.8+.37	6.6- 7.0	0.53	7.81	11	7.1+.09	6.6- 7.6	0.29	4.06	
M ¹ - ⁴	2	4.4+.33	4.2- 4.5	0.47	10.73	11	4.3+.04	4.1- 4.5	0.14	5.35	
M ¹ - ³	3	4.0+.12	3.8- 4.2	0.21	5.30	11	3.9+.04	3.7- 4.1	0.12	3.13	
R-LM ³	2	6.5+.27	6.4- 6.6	0.38	5.78	10	6.4+.04	6.3- 6.6	0.12	1.84	
FM	2	3.9+.22	3.8- 3.9	0.32	8.11	10	3.9+.08	3.5- 4.2	0.24	6.15	
IO	2	4.4+.22	4.3- 4.4	0.32	7.19	11	4.3+.08	3.9- 4.7	0.26	5.95	
VV	2	4.2+.50	3.8- 4.5	0.71	16.84	11	4.5+.09	4.1- 5.0	0.31	6.96	
DL	2	14.4+.33	14.2-14.5	0.47	3.28	11	14.2+.16	13.7-15.5	0.53	3.73	
I ₁ -M ₄	2	8.1+.43	7.8- 8.3	0.60	7.41	11	8.3+.11	7.7- 8.9	0.36	4.33	
M ₁ - ₄	2	4.6+.27	4.5- 4.7	0.38	8.17	10	4.7+.07	4.4- 5.0	0.21	4.40	
M ₁ - ₃	3	3.5+.14	3.4- 3.8	0.23	6.69	10	3.7+.06	3.3- 3.9	0.20	6.51	
C-AP	2	4.3+.33	4.1- 4.4	0.47	10.98	11	4.4+.06	3.9- 4.6	0.20	4.93	
C-AR	2	4.6+.33	4.4- 4.7	0.47	10.27	11	4.2+.07	3.3- 4.6	0.23	5.48	
NL	2	7.8+.43	7.5- 8.0	0.60	7.69	10	7.6+.13	7.0- 8.4	0.41	5.43	
NW	2	3.1+.33	2.9- 3.2	0.47	15.23	10	3.1+.07	2.8- 3.5	0.22	7.06	
NWMN	2	1.5+.27	1.4- 1.6	0.38	25.07	10	1.3+.04	1.2- 1.5	0.12	9.38	
PN	2	3.2+.27	3.1- 3.3	0.38	11.75	10	2.8+.06	2.4- 3.6	0.18	6.54	
PLF-AB	2	4.4+.27	4.3- 4.5	0.37	8.55	10	4.6+.14	4.4- 4.8	0.43	9.41	
SD	2	5.1+.22	5.0- 5.1	0.32	6.20	11	4.6+.08	4.2- 5.0	0.26	5.52	

TABLE 1 (cont'd)

	N	$\bar{x} \pm T$	OR	s	CV		N	$\bar{x} \pm T$	OR	s	CV
P. maculata (Arakun Mission)						P. ingrami (total)					
BL	3	17.2 \pm .42	16.4-17.7	0.72	4.21	11	15.9 \pm .16	14.8-17.3	0.52	3.25	
ZW	3	9.9 \pm .26	9.4-10.3	0.45	4.57	14	9.2 \pm .20	8.4-10.9	0.76	8.26	
OBW	3	7.1 \pm .14	6.8- 7.2	0.23	3.30	14	7.0 \pm .10	6.5- 7.9	0.39	5.59	
IBW	3	2.4 \pm .21	2.1- 2.8	0.36	15.00	12	2.4 \pm .09	1.8- 2.9	0.32	13.53	
C ¹ -M ⁴	3	6.7 \pm .12	6.5- 6.9	0.21	3.16	15	5.9 \pm .08	5.4- 6.5	0.31	5.30	
M ¹⁻⁴	3	4.2 \pm .04	4.1- 4.2	0.07	1.67	15	3.6 \pm .04	3.2- 3.8	0.16	4.45	
M ¹⁻³	3	3.8 \pm .0	-	-	-	16	3.3 \pm .04	2.9- 3.5	0.16	4.94	
R-LM ³	3	6.0 \pm .12	5.8- 6.2	0.20	3.33	15	5.4 \pm .07	4.8- 6.2	0.29	5.33	
FM	3	3.8 \pm .04	3.7- 3.8	0.07	1.84	12	3.6 \pm .04	3.4- 3.8	0.14	3.84	
IO	3	3.9 \pm .04	3.8- 3.9	0.07	1.79	15	3.9 \pm .06	3.4- 4.2	0.24	6.05	
VV	3	4.1 \pm .22	3.8- 4.5	0.38	9.29	14	3.7 \pm .09	3.3- 4.6	0.35	9.57	
DL	3	13.2 \pm .25	12.7-13.5	0.44	3.30	14	11.8 \pm .19	10.4-13.7	0.71	6.00	
I ₁ -M ₄	3	7.8 \pm .15	7.6- 8.1	0.25	3.27	15	6.8 \pm .07	6.3- 7.3	0.27	3.95	
M ₁₋₄	3	4.6 \pm .04	4.5- 4.6	0.07	1.52	15	4.0 \pm .04	3.7- 4.2	0.15	3.77	
M ₁₋₃	3	3.5 \pm .04	3.5- 3.6	0.07	2.00	15	3.1 \pm .04	2.7- 3.3	0.15	4.78	
C-AP	3	4.0 \pm .12	3.8- 4.2	0.20	5.00	13	3.6 \pm .08	3.2- 4.0	0.29	7.93	
C-AR	3	4.2 \pm .12	4.0- 4.4	0.21	5.05	14	3.4 \pm .10	2.8- 4.0	0.36	10.72	
NL	2	6.7 \pm .26	6.4- 6.9	0.36	5.31	14	6.3 \pm .14	5.4- 7.5	0.53	8.49	
NW	3	2.8 \pm .15	2.6- 3.1	0.25	9.10	14	2.9 \pm .09	2.3- 3.5	0.32	11.07	
NWMN	2	1.4 \pm .07	1.3- 1.4	0.10	7.14	14	1.3 \pm .04	1.0- 1.5	0.15	11.87	
PN	2	2.9 \pm .07	2.8- 2.9	0.10	3.45	14	2.2 \pm .10	1.7- 2.8	0.36	16.39	
PLF-AB	3	4.1 \pm .15	3.8- 4.3	0.25	6.22	13	4.5 \pm .05	4.1- 4.7	0.19	4.16	
SD	3	4.5 \pm .10	4.3- 4.6	0.17	3.84	13	3.5 \pm .08	3.2- 4.2	0.30	8.61	
P. i. (Richmond)						P. i. (Normanton)					
BL	4	15.9 \pm .20	15.4-17.1	0.40	2.49	3	16.1 \pm .67	15.0-17.3	1.15	9.40	
ZW	5	9.0 \pm .21	8.5- 9.8	0.47	5.27	4	9.8 \pm .57	8.4-10.9	1.14	11.65	
OBW	5	7.1 \pm .12	6.8- 7.4	0.28	3.92	4	7.2 \pm .34	6.5- 7.9	0.68	9.45	
IBW	5	2.2 \pm .14	1.8- 2.6	0.31	14.00	3	2.7 \pm .17	2.4- 2.9	0.29	10.80	
C ¹ -M ⁴	5	5.9 \pm .06	5.7- 6.0	0.14	2.39	4	6.2 \pm .13	5.9- 6.5	0.25	4.06	
M ¹⁻⁴	5	3.6 \pm .17	3.4- 3.7	0.39	10.75	4	3.8 \pm .04	3.7- 3.8	0.08	2.14	
M ¹⁻³	5	3.3 \pm .05	3.1- 3.4	0.11	3.39	4	3.4 \pm .06	3.3- 3.5	0.10	2.94	
R-LM ³	5	5.4 \pm .09	5.1- 5.6	0.21	3.93	4	5.7 \pm .16	5.2- 6.2	0.31	5.48	
FM	4	3.8 \pm .03	3.7- 3.8	0.06	1.50	3	3.6 \pm .04	3.5- 3.6	0.07	1.94	
IO	5	3.8 \pm .06	3.7- 4.0	0.13	3.48	4	3.9 \pm .20	3.4- 4.2	0.40	10.51	
VV	4	3.7 \pm .12	3.4- 3.9	0.24	6.59	4	4.0 \pm .24	3.6- 4.6	0.49	12.23	
DL	4	11.9 \pm .30	11.4-12.8	0.61	5.11	4	12.4 \pm .68	10.9-13.7	1.36	11.01	
I ₁ -M ₄	5	6.9 \pm .09	6.6- 7.1	0.20	2.90	4	7.1 \pm .20	6.7- 7.3	0.41	5.74	
M ₁₋₄	5	4.0 \pm .03	3.9- 4.0	0.07	1.75	4	4.2 \pm .04	4.1- 4.2	0.08	1.93	
M ₁₋₃	5	3.0 \pm .03	3.0- 3.1	0.07	2.33	4	3.2 \pm .04	3.1- 3.3	0.08	2.54	
C-AP	3	3.6 \pm .06	3.5- 3.7	0.10	2.78	4	3.8 \pm .13	3.4- 4.0	0.26	6.96	
C-AR	4	3.4 \pm .22	3.1- 4.0	0.44	12.93	4	3.7 \pm .16	3.3- 4.0	0.31	8.40	
NL	4	6.3 \pm .18	5.9- 6.6	0.36	5.70	4	6.8 \pm .12	6.3- 7.5	0.24	3.59	
NW	4	2.9 \pm .13	2.6- 3.2	0.25	8.67	4	3.0 \pm .28	2.3- 3.5	0.57	18.83	
NWMN	4	1.2 \pm .05	1.1- 1.3	0.10	8.33	4	1.2 \pm .10	1.0- 1.5	0.21	17.33	
PN	4	2.3 \pm .11	2.0- 2.5	0.22	9.72	4	2.5 \pm .17	2.0- 2.8	0.34	13.66	
PLF-AB	4	4.6 \pm .05	4.5- 4.7	0.10	2.17	4	4.4 \pm .09	4.2- 4.6	0.18	4.15	
SD	4	3.4 \pm .10	3.2- 3.7	0.21	6.12	4	3.8 \pm .19	3.3- 4.2	0.37	9.84	
P. i. (201km W. of Burketown)						P. i. (owl pellet, Barkly Tbl'd)					
BL	2	15.4 \pm .45	14.8-15.9	0.78	5.07	8	5.4 \pm .08	5.3- 5.6	0.11	2.09	
ZW	3	8.8 \pm .21	8.5- 9.2	0.36	4.10	8	3.4 \pm .04	3.3- 3.6	0.11	3.32	
OBW	3	6.9 \pm .10	6.8- 7.1	0.17	2.51	8	3.1 \pm .05	2.9- 3.3	0.13	4.22	
IBW	2	2.1 \pm .0	2.2- 2.2	-	-						
C ¹ -M ⁴	3	5.5 \pm .14	5.4- 5.8	0.23	4.26	5	3.5 \pm .09	3.3- 3.8	0.20	5.71	
M ¹⁻⁴	3	3.4 \pm .12	3.2- 3.6	0.21	6.24	15	10.9 \pm .08	10.5-11.5	0.31	2.89	
M ¹⁻³	3	3.1 \pm .12	2.9- 3.3	0.20	6.45	15	6.2 \pm .05	6.0- 6.6	0.18	2.83	
R-LM ³	3	5.2 \pm .09	5.1- 5.4	0.16	3.04	16	3.7 \pm .04	3.6- 4.1	0.15	4.00	
FM	3	3.6 \pm .09	3.4- 3.7	0.16	4.39	16	2.9 \pm .02	2.8- 3.1	0.10	3.32	
IO	3	3.8 \pm .10	3.7- 4.0	0.17	4.55	13	3.3 \pm .04	3.0- 3.5	0.16	4.87	
VV	3	3.4 \pm .07	3.3- 3.5	0.12	3.60	17	3.1 \pm .04	2.8- 3.4	0.18	4.42	
DL	3	11.2 \pm .26	10.7-11.6	0.46	4.09						
I ₁ -M ₄	3	6.5 \pm .12	6.3- 6.7	0.20	3.08						
M ₁₋₄	3	3.9 \pm .09	3.7- 4.0	0.16	4.05						
M ₁₋₃	3	2.9 \pm .12	2.7- 3.1	0.20	6.90						
C-AP	3	3.5 \pm .04	3.5- 3.6	0.07	2.00						
C-AR	3	3.3 \pm .04	3.2- 3.3	0.07	2.12						
NL	3	5.8 \pm .07	5.7- 5.9	0.12	2.11						
NW	3	2.9 \pm .04	2.9- 3.0	0.07	2.41						
NWMN	3	1.2 \pm .04	1.2- 1.3	0.07	3.83						
PN	3	1.9 \pm .07	1.8- 2.0	0.12	6.42						
PLF-AB	3	4.4 \pm .17	4.1- 4.7	0.30	6.81						
SD	3	3.3 \pm .07	3.2- 3.4	0.12	3.70						

N	$\bar{x} \pm \tau$	OR	s	CV	N	$\bar{x} \pm \tau$	OR	s	CV
P. tenuirostris					P. gilesi				
8	16.3 \pm .27	15.2-17.4	0.76	4.67	4	18.4 \pm .65	16.6-19.4	1.31	7.11
8	8.7 \pm .13	8.3- 9.3	0.36	4.10	3	10.6 \pm .64	9.5-11.7	1.10	10.40
9	6.5 \pm .09	6.2- 6.9	0.27	4.11	4	7.6 \pm .23	6.9- 8.0	0.47	6.17
9	2.3 \pm .05	2.1- 2.5	0.15	6.70	4	2.8 \pm .05	2.7- 2.9	0.10	3.57
12	6.1 \pm .06	5.8- 6.3	0.20	3.24	5	7.0 \pm .24	6.2- 7.6	0.53	7.56
12	3.7 \pm .04	3.4- 3.8	0.15	4.00	5	4.4 \pm .14	4.0- 4.8	0.30	6.91
12	3.3 \pm .03	3.1- 3.5	0.12	3.65	5	3.9 \pm .13	3.5- 4.3	0.29	7.36
11	5.5 \pm .06	5.2- 5.8	0.19	3.40	5	6.4 \pm .18	5.7- 6.7	0.40	6.20
7	3.6 \pm .05	3.5- 3.8	0.13	3.58	4	3.8 \pm .07	3.7- 4.0	0.15	3.97
11	3.7 \pm .04	3.5- 4.0	0.14	3.70	5	4.3 \pm .07	4.1- 4.5	0.16	3.67
9	3.9 \pm .08	3.5- 4.2	0.23	5.87	5	4.4 \pm .18	4.0- 4.9	0.39	8.95
12	12.2 \pm .13	11.4-13.0	0.45	3.71	5	14.1 \pm .40	12.7-15.0	0.89	6.33
12	7.1 \pm .08	6.6- 7.4	0.28	4.01	5	8.2 \pm .14	7.7- 8.9	0.31	3.81
13	4.1 \pm .07	3.8- 4.8	0.25	6.06	5	4.7 \pm .16	4.3- 5.1	0.36	7.74
13	3.1 \pm .04	2.9- 3.8	0.15	4.75	5	3.6 \pm .11	3.3- 3.9	0.24	5.95
11	3.5 \pm .03	3.3- 3.7	0.11	3.11	4	4.1 \pm .18	3.6- 4.3	0.35	8.55
12	3.4 \pm .06	3.1- 3.7	0.21	6.08	5	4.0 \pm .13	3.7- 4.4	0.30	7.50
11	6.7 \pm .16	5.8- 7.6	0.54	8.06	5	7.7 \pm .23	6.9- 8.3	0.50	6.56
7	2.7 \pm .09	2.4- 3.2	0.23	8.60	5	3.2 \pm .06	3.0- 3.4	0.14	4.41
10	1.0 \pm .05	0.8- 1.2	0.15	14.53	4	1.4 \pm .12	1.0- 1.5	0.24	17.49
10	2.4 \pm .06	2.1- 2.7	0.19	7.97	3	2.9 \pm .14	2.8- 3.2	0.23	8.07
10	4.2 \pm .08	3.7- 4.5	0.24	5.66	4	4.8 \pm .10	4.5- 4.9	0.20	4.17
10	3.9 \pm .07	3.6- 4.1	0.21	5.27	4	3.9 \pm .04	3.8- 4.0	0.09	2.21
P. i.(subtilissima form)									
15.5									
8.8									
6.8									
2.2									
5.8									
2.5									
3.2									
5.2									
3.5									
4.1									
3.7									
11.6									
6.8									
4.0									
3.1									
3.5									
3.3									
6.2									
2.9									
1.3									
1.7									
4.4									
3.5									
P. i.brunneus Holotype					P. t.Holotype				
8.9									
6.8									

TABLE 2: RATIOS OF CRANIAL, DENTAL AND EXTERNAL CHARACTERS IN *Planigale*

Locality names have been abbreviated as follows: Mt Molloy, Qd: Townsville, Qd: Humpty Doo, N.T.: Aurukun Mission, Qd: Richmond, Qd: Karumba, Qd: 200 km west of Burketown in N.T.; Brunette Downs, N.T.: fossil Kimberleys sample from surface of cave in southern Kimberleys. X, sample mean; N, sample number; O.R., observed range; TV, tail-vent length; HB, head-body length (nose to vent); HF, hind-foot length; ST, length of supratragus of ear; E, ear (tip of pinna to notch). Other abbreviations as in Table 1.

	BL/ZV	IO/ZV	BR/ZV	BL/H-1-13	SD/ZV	SD/BL	SD/C-1-13	SD/IO	FM/SD	FM/ZV	MZ/ $\frac{1}{E}$
<u><i>Planigale novaeguineae</i></u>											
All	\bar{x} (N) 1.74 (2) O.R. 1.73-1.74	0.41 (2) 0.36-0.45	1.13 (2) 1.12-1.14	1.09 (2) 1.07-1.10	0.49 (2) 0.43-0.49	0.28 (2) 0.28	0.72 (2) 0.71-0.73	1.23 (2) 1.12-1.34	0.70 (2) 0.71-0.73	0.35 (2) 0.34-0.36	0.36 (2) 0.34-0.37
<u><i>P. maculata</i></u>											
All	\bar{x} (N) 1.73 (31) O.R. 1.60-1.80	0.40 (34) 0.35-0.44	1.20 (32) 1.05-1.34	1.13 (31) 1.03-1.24	0.45 (34) 0.41-0.51	0.26 (31) 0.23-0.28	0.70 (34) 0.59-0.78	1.13 (33) 0.96-1.34	0.80 (31) 0.70-1.00	0.36 (31) 0.32-0.41	0.37 (35) 0.33-0.42
<u><i>P. maculata</i></u>											
All Queensland	\bar{x} (N) 1.73 (22) O.R. 1.60-1.80	0.40 (24) 0.35-0.44	1.18 (22) 1.05-1.37	1.10 (22) 1.03-1.16	0.47 (24) 0.42-0.51	0.27 (22) 0.25-0.28	0.72 (24) 0.66-0.78	1.16 (23) 0.96-1.34	0.78 (22) 0.70-0.89	0.36 (22) 0.32-0.41	0.37 (25) 0.33-0.42
<u><i>P. maculata</i></u>											
Mt. Molloy	\bar{x} (N) 1.72 (7) O.R. 1.68-1.77	0.41 (7) 0.38-0.43	1.20 (6) 1.15-1.28	1.11 (7) 1.07-1.15	0.46 (7) 0.44-0.48	0.27 (7) 0.26-0.27	0.70 (7) 0.67-0.73	1.12 (7) 1.09-1.18	0.78 (7) 0.70-0.86	0.35 (7) 0.32-0.41	0.37 (7) 0.34-0.40
<u><i>P. maculata</i></u>											
Townsville	\bar{x} (N) 1.72 (2) O.R. 1.69-1.74	0.40 (2) 0.40	1.17 (2) 1.15-1.18	1.13 (2) 1.13	0.46 (2) 0.46	0.28 (2) 0.28	0.76 (2) 0.76	1.16 (2) 1.16	0.77 (2) 0.77	0.36 (2) 0.35-0.36	0.36 (2) 0.35-0.37
<u><i>P. maculata</i></u>											
All N. Territory	\bar{x} (N) 1.72 (9) O.R. 1.65-1.80	0.40 (10) 0.35-0.44	1.24 (10) 1.05-1.33	1.19 (9) 1.13-1.24	0.43 (10) 0.41-0.47	0.25 (9) 0.23-0.26	0.65 (10) 0.59-0.68	1.07 (10) 0.96-1.15	0.85 (9) 0.75-1.00	0.36 (9) 0.32-0.42	0.36 (10) 0.33-0.41
<u><i>P. maculata</i></u>											
Humpty Doo	\bar{x} (N) 1.73 (5) O.R. 1.65-1.80	0.42 (6) 0.38-0.44	1.22 (6) 1.05-1.33	1.17 (5) 1.13-1.21	0.43 (6) 0.41-0.45	0.24 (5) 0.23-0.25	1.05 (6) 0.96-1.14	0.89 (5) 0.78-1.00	0.38 (5) 0.36-0.42	0.37 (6) 0.35-0.41	0.37 (6) 0.35-0.41
<u><i>P. maculata</i></u>											
Aurukun	\bar{x} (N) 1.75 (3) O.R. 1.71-1.79	0.39 (3) 0.38-0.40	1.23 (3) 1.16-1.34	1.07 (3) 1.00-1.13	0.46 (3) 0.45-0.47	0.26 (3) 0.26	0.67 (3) 0.66-0.70	1.16 (3) 1.13-1.18	0.84 (3) 0.83-0.86	0.38 (3) 0.31-0.39	0.38 (3) 0.37-0.40
<u><i>P. tenuirostris</i></u>											
All	\bar{x} (N) 1.87 (8) O.R. 1.76-1.98	0.43 (8) 0.43-0.45	1.26 (9) 1.18-1.34	1.27 (10) 1.18-1.34	0.44 (8) 0.43-0.46	0.24 (8) 0.22-0.25	0.64 (10) 0.59-0.62	1.03 (9) 0.95-1.09	0.95 (7) 0.85-1.03	0.42 (7) 0.38-0.45	0.39 (8) 0.36-0.41
<u><i>P. ingrami</i></u>											
All	\bar{x} (N) 1.72 (9) O.R. 1.65-1.84	0.42 (11) 0.39-0.44	1.44 (11) 1.30-1.61	1.37 (11) 1.24-1.52	0.38 (11) 0.36-0.40	0.22 (9) 0.21-0.23	0.60 (11) 0.53-0.65	0.91 (11) 0.85-1.00	1.06 (10) 0.95-1.16	0.40 (10) 0.34-0.45	0.35 (12) 0.32-0.40
<u><i>P. ingrami</i></u>											
Richmond	\bar{x} (N) 1.76 (4) O.R. 1.71-1.84	0.43 (4) 0.40-0.44	1.48 (5) 1.38-1.61	1.37 (4) 1.33-1.42	0.30 (4) 0.36-0.40	0.22 (4) 0.21-0.22	0.58 (4) 0.59-0.62	0.89 (4) 0.84-0.95	1.11 (4) 1.03-1.16	0.42 (4) 0.39-0.45	0.37 (5) 0.34-0.40
<u><i>P. ingrami</i></u>											
Karumba	\bar{x} (N) 1.69 (2) O.R. 1.65-1.72	0.40 (3) 0.39-0.40	1.37 (3) 1.30-1.43	1.31 (3) 1.30-1.32	0.39 (3) 0.36-0.40	0.23 (3) 0.22-0.23	0.62 (3) 0.61-0.65	0.97 (3) 0.91-1.00	0.95 (2) 0.95	0.37 (2) 0.34-0.38	0.33 (3) 0.32-0.36
<u><i>P. ingrami</i></u>											
Burketown	\bar{x} (N) 1.72 (2) O.R. 1.70-1.73	0.44 (3) 0.43-0.44	0.53 (2) 0.53	1.49 (2) 1.39-1.58	1.43 (3) 1.24-1.52	0.22 (2) 0.21-0.22	0.59 (3) 0.59	0.96 (3) 0.85-0.97	1.10 (3) 1.00-1.16	0.41 (3) 0.37-0.43	0.35 (3) 0.34-0.38
<u><i>P. ingrami</i></u>											
Brunette Downs	\bar{x} (N) - O.R. -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
<u><i>P. ingrami</i></u>											
Kimberleys	\bar{x} (N) 1.76 (1) O.R. 1.76	0.47 (1) 0.47	0.52 (1) 0.52	1.44 (1) 1.44	1.38 (1) 1.38	0.23 (1) 0.23	0.60 (1) 0.60	0.85 (1) 0.85	1.00 (1) 1.00	0.40 (1) 0.40	0.36 (1) 0.36
<u><i>P. ingrami</i></u>											
Fossil, Kimberleys	\bar{x} (N) - O.R. -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
<u><i>P. gilesi</i></u>											
All	\bar{x} (N) 1.73 (4) O.R. 1.66-1.80	0.40 (4) 0.37-0.43	0.45 (4) 0.41-0.50	1.22 (4) 1.14-1.28	1.23 (4) 1.14-1.29	0.22 (4) 0.21-0.23	0.57 (4) 0.53-0.61	0.94 (4) 0.91-0.98	0.98 (4) 0.93-1.03	0.36 (4) 0.32-0.41	0.37 (4) 0.33-0.40
WM3432 Tambrey, W.A.	1.69	.39	.42	1.32	-	0.24	0.65	1.02	0.93	0.37	0.32

	$\frac{C_d}{C_u} \left(\frac{C_d}{C_u} \right)_M$	$\frac{I_d}{I_u} \left(\frac{I_d}{I_u} \right)_M$	TL/BL	NZ/NN	NN/NL	TN/NL	TN/NL	VL/DL	DL/BL	TL/UL	HL/HL	SL/SL
<u>Planigale novaeguineae</u>												
All	0.82 (2) 0.79-0.84	1.05 (2) 1.03-1.07	0.42 (2) 0.42	0.31 (2) 0.30-0.32	0.43 (2) 0.41-0.44	0.39 (2) 0.36-0.41	0.26 (2) 0.24-0.28	0.78 (2) 0.77-0.79	0.86 (4) 0.84-0.87	0.14 (3) 0.14-0.15	-	-
<u>P. maculata</u>												
All	0.69 (36) 0.61-0.82	0.96 (36) 0.78-1.09	0.41 (31) 0.38-0.44	0.28 (34) 0.25-0.33	0.40 (34) 0.34-0.45	0.41 (33) 0.32-0.48	0.25 (31) 0.21-0.29	0.77 (31) 0.74-0.84	0.85 (15) 0.70-1.04	0.17 (15) 0.14-0.20	0.32 (5) 0.27-0.36	
<u>P. maculata</u>												
All Queensland	0.67 (26) 0.61-0.82	0.95 (27) 0.78-1.07	0.41 (22) 0.39-0.44	0.28 (25) 0.23-0.33	0.40 (25) 0.34-0.45	0.41 (25) 0.34-0.47	0.25 (22) 0.21-0.29	0.77 (22) 0.74-0.84	0.82 (13) 0.70-0.90	0.17 (13) 0.14-0.20	0.32 (5) 0.27-0.36	
<u>P. maculata</u>												
Nt. Molloy,	0.68 (7) 0.61-0.73	0.98 (7) 0.92-1.05	0.42 (7) 0.41-0.43	0.26 (7) 0.23-0.28	0.36 (7) 0.35-0.38	0.41 (7) 0.33-0.47	0.25 (7) 0.23-0.29	0.76 (7) 0.75-0.77	0.82 (5) 0.70-0.90	0.17 (5) 0.16-0.19	0.34 (2) 0.33-0.35	
<u>P. maculata</u>												
Townsville	0.62 (2) 0.61-0.63	0.97 (2) 0.97	0.42 (2) 0.39-0.44	0.28 (2) 0.27-0.29	0.40 (2) 0.36-0.43	0.41 (2) 0.41	0.21 (2) 0.21	0.78 (2) 0.78	0.75 (1) 0.75	0.14 (1) 0.14	-	-
<u>P. maculata</u>												
All N. Territory	0.73 (10) 0.63-0.80	0.98 (9) 0.87-1.09	0.41 (9) 0.38-0.43	0.29 (9) 0.26-0.33	0.41 (9) 0.38-0.44	0.41 (8) 0.32-0.48	0.24 (9) 0.22-0.25	0.77 (9) 0.75-0.78	1.04 (2) 1.04	0.16 (2) 0.15-0.16	-	-
<u>P. maculata</u>												
Humpty Do	0.73 (6) 0.63-0.80	0.96 (5) 0.87-1.08	0.41 (5) 0.40-0.43	0.30 (5) 0.28-0.33	0.41 (5) 0.38-0.43	0.43 (4) 0.33-0.48	0.24 (5) 0.23-0.25	0.77 (5) 0.75-0.73	1.04 (1) 1.04	0.15 (1) 0.15	-	-
<u>P. maculata</u>												
Arafura	0.66 (3) 0.63-0.71	0.92 (3) 0.83-1.00	0.39 (2) 0.39	0.29 (3) 0.26-0.30	0.45 (2) 0.44-0.45	0.43 (2) 0.41-0.45	0.23 (3) 0.22-0.25	0.77 (3) 0.76-0.77	0.77 (4) 0.71-0.82	0.16 (4) 0.14-0.17	0.28 (3) 0.26-0.30	
<u>P. tenuirostris</u>												
All	0.72 (12) 0.67-0.78	1.01 (12) 0.87-1.13	0.41 (8) 0.38-0.46	0.32 (8) 0.29-0.36	0.41 (11) 0.36-0.45	0.35 (10) 0.31-0.42	0.23 (8) 0.21-0.24	0.75 (8) 0.73-0.76	0.87 (4) 0.78-0.95	0.17 (4) 0.15-0.19	0.28 (4) 0.26-0.30	
<u>P. ingrami</u>												
All	0.69 (20) 0.55-0.77	0.87 (27) 0.77-1.03	0.39 (9) 0.37-0.42	0.32 (11) 0.28-0.34	0.47 (11) 0.43-0.51	0.36 (11) 0.31-0.41	0.23 (9) 0.20-0.25	0.75 (9) 0.73-0.76	1.05 (3) 0.90-1.13	0.15 (6) 0.12-0.18	0.35 (3) 0.31-0.38	
<u>P. ingrami</u>												
Richmond	0.70 (5) 0.65-0.73	0.95 (5) 0.90-1.03	0.40 (4) 0.38-0.42	0.32 (4) 0.31-0.33	0.46 (4) 0.43-0.49	0.37 (4) 0.34-0.38	0.23 (4) 0.20-0.25	0.75 (3) 0.73-0.76	1.06 (2) 1.00-1.11	0.18 (2) 0.17-0.18	-	-
<u>P. ingrami</u>												
Karumba	0.75 (3) 0.73-0.77	0.93 (3) 0.89-0.97	0.40 (2) 0.39-0.40	0.31 (3) 0.28-0.33	0.46 (3) 0.41-0.51	0.39 (3) 0.35-0.41	0.24 (2) 0.23-0.24	0.76 (2) 0.75-0.76	1.00 (3) 0.90-1.12	0.13 (3) 0.12-0.15	0.35 (3) 0.33-0.38	
<u>P. ingrami</u>												
Burketown	0.68 (3) 0.55-0.76	0.91 (3) 0.87-0.96	0.38 (2) 0.37-0.39	0.33 (3) 0.33-0.34	0.50 (3) 0.49-0.51	0.32 (3) 0.31-0.34	0.22 (2) 0.22	0.75 (2) 0.73-0.76	1.10 (3) 1.07-1.13	0.16 (3) 0.15-0.17	0.33 (3) 0.31-0.35	
<u>P. ingrami</u>												
Bruntate Downs	0.66 (8) 0.58-0.73	0.87 (15) 0.77-0.93	- -	- -	- -	- -	- -	- -	- -	- -	- -	-
<u>P. ingrami</u>												
Kimberleys	0.72 (1) 0.72	0.90 (1) 0.90	0.40 (1) 0.40	0.33 (1) 0.33	0.47 (1) 0.47	0.27 (1) 0.27	0.24 (1) 0.24	0.75 (1) 0.75	1.12 (2) 1.06-1.18	0.18 (2) 0.17-0.18	0.38 (2) 0.36-0.39	
<u>P. ingrami</u>												
Fossil, Kimberleys	- -	0.79 (9) 0.75-0.90	- -	- -	- -	- -	- -	- -	- -	- -	- -	-
<u>P. gilesi</u>												
All	0.66 (5) 0.63-0.71	0.95 (5) 0.89-1.03	0.42 (4) 0.40-0.43	0.30 (4) 0.27-0.32	0.42 (5) 0.39-0.45	0.39 (4) 0.36-0.41	0.25 (4) 0.22-0.27	0.77 (4) 0.76-0.77	0.94 (6) 0.77-1.02	0.15 (7) 0.14-0.17	0.36 (4) 0.33-0.38	
WAM3432 Tambrey, W.A.	0.82	0.74	0.40	0.32	0.47	0.34	0.22	0.97	-	-	-	-

PLATE 43

A-D, *Planigale maculata* (typical form). J16477, adult, Mt Molloy, Qd. A, $\times 5.1$. B-D, $\times 3.7$.

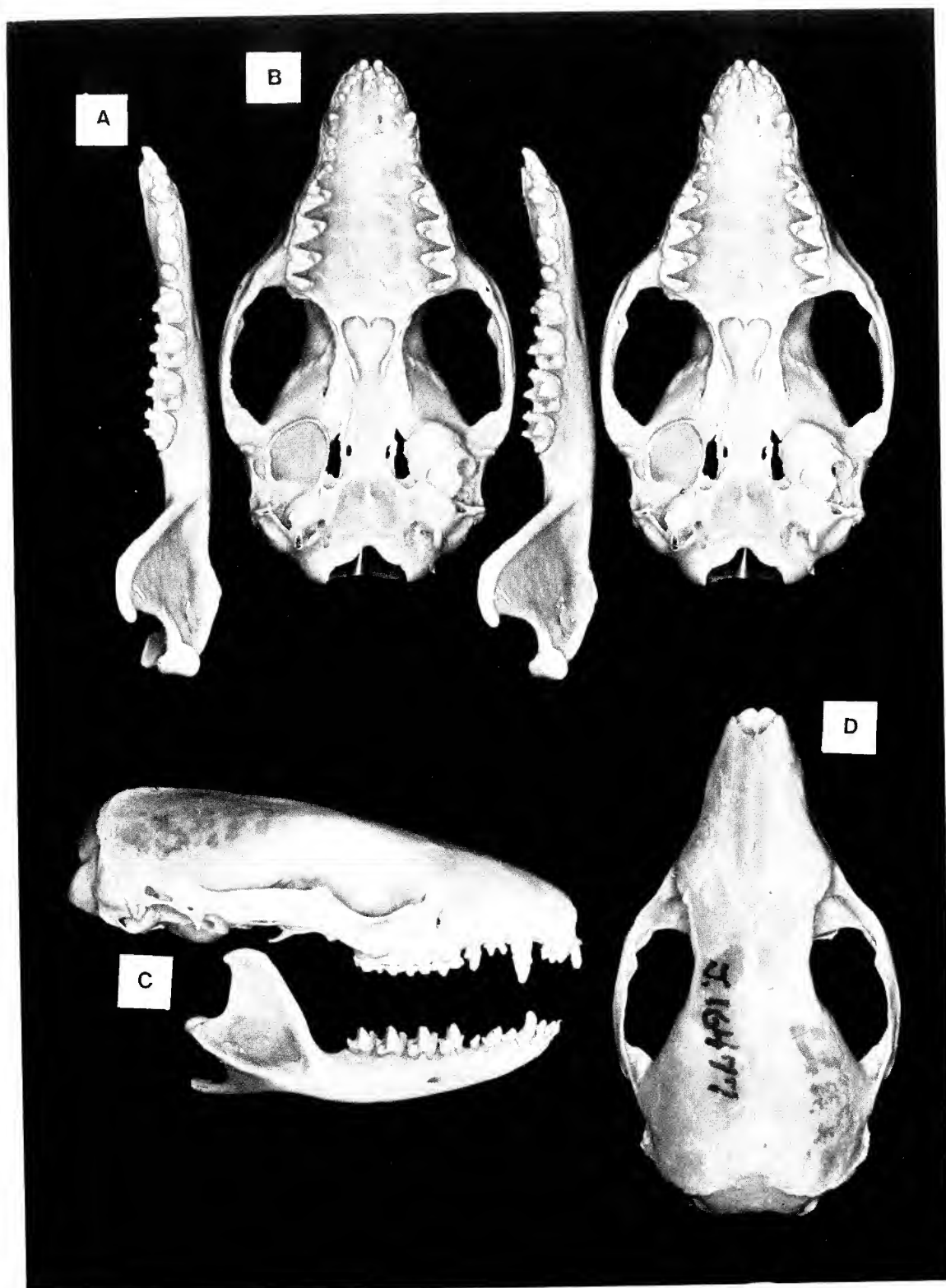


PLATE 44

A-D, *Planigale maculata* (*sinualis* form). WAM M8095, adult, Humpty Doo, N.T. A, \times 5.6. B-D, \times 3.8.

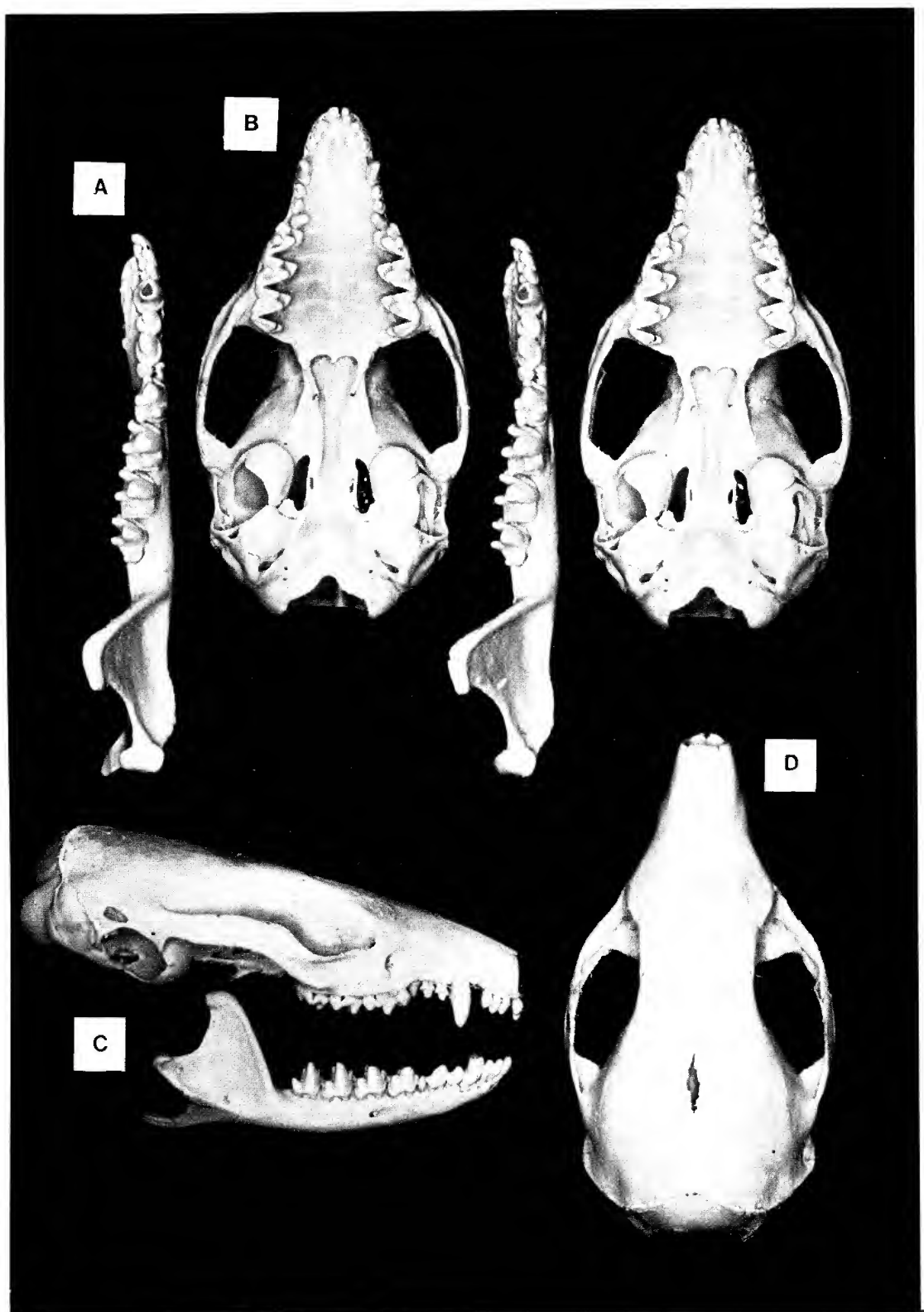


PLATE 45

A–D, *Planigale novaeguineae*. J4368, adult, New Guinea. A,
× 4·6. B–D, × 3·6.

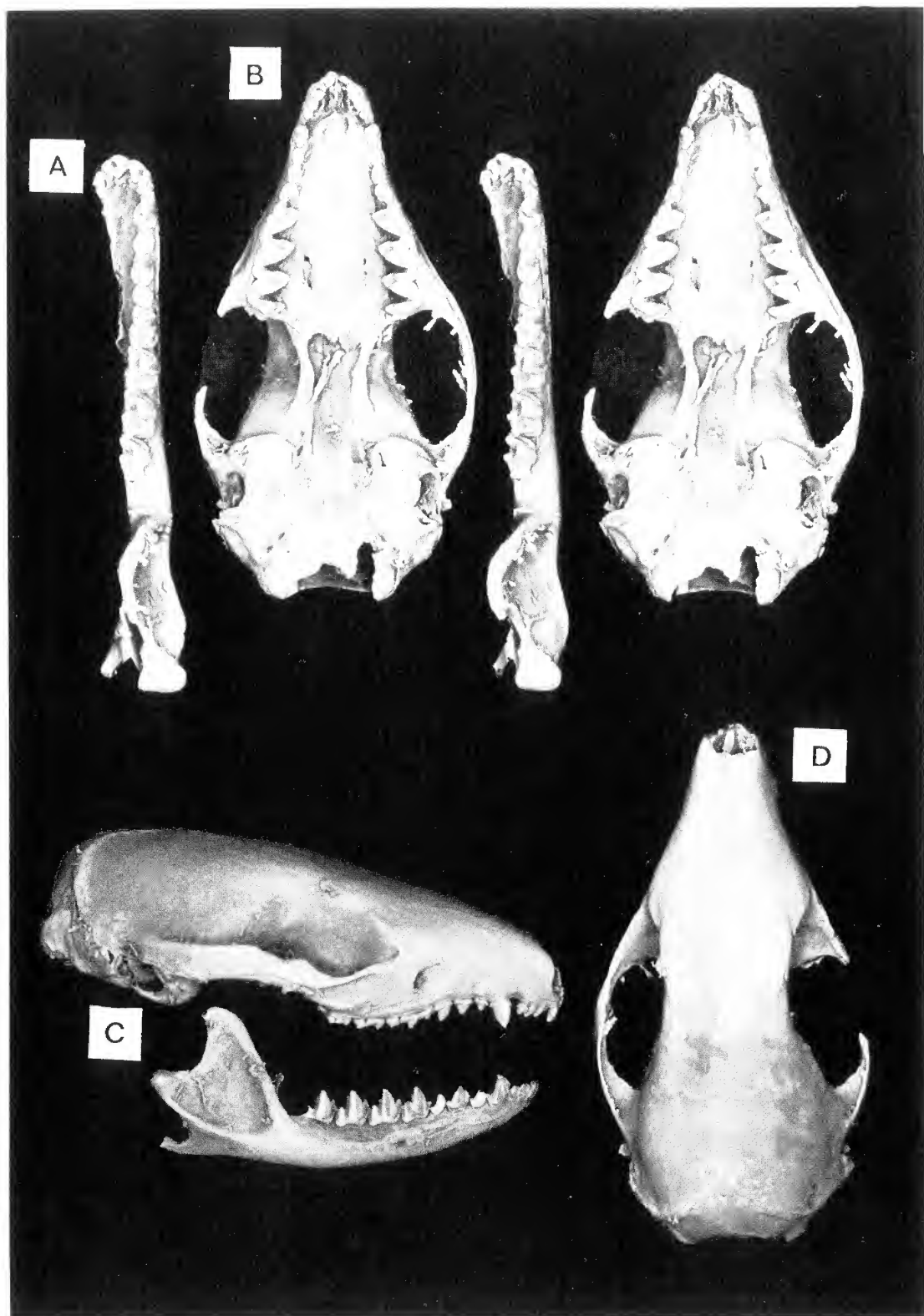


PLATE 46

A-D. *Planigale ingrami* (typical form), JM824, adult, nr
Richmond, Qd. A, $\times 6.8$. B-D, $\times 4.7$.

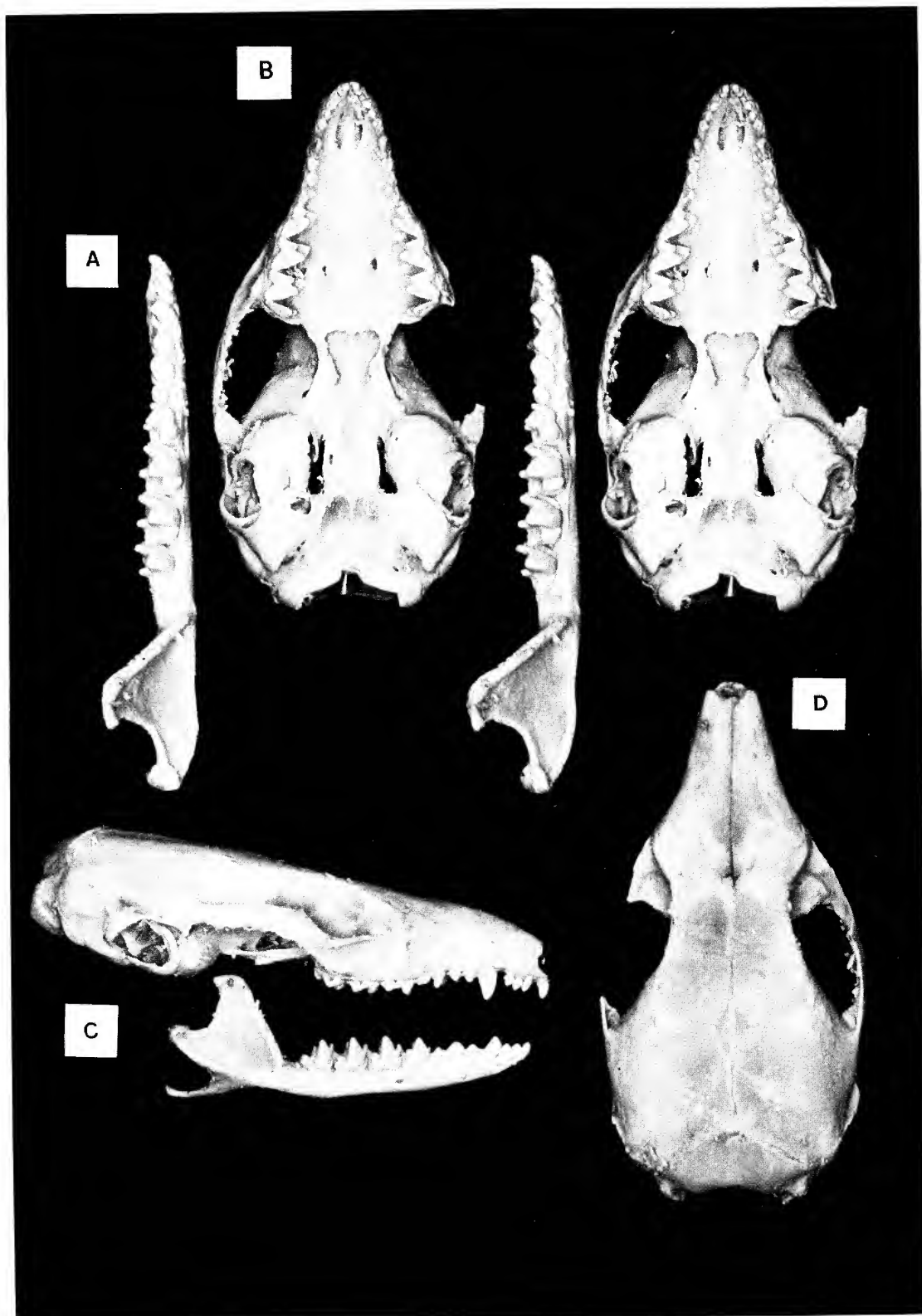


PLATE 47

A-D. *Planigale ingrami* (*subtilissima* form). WAM M2846,
Ord River area, W.A. A, $\times 6.8$. B-D, $\times 4.7$.

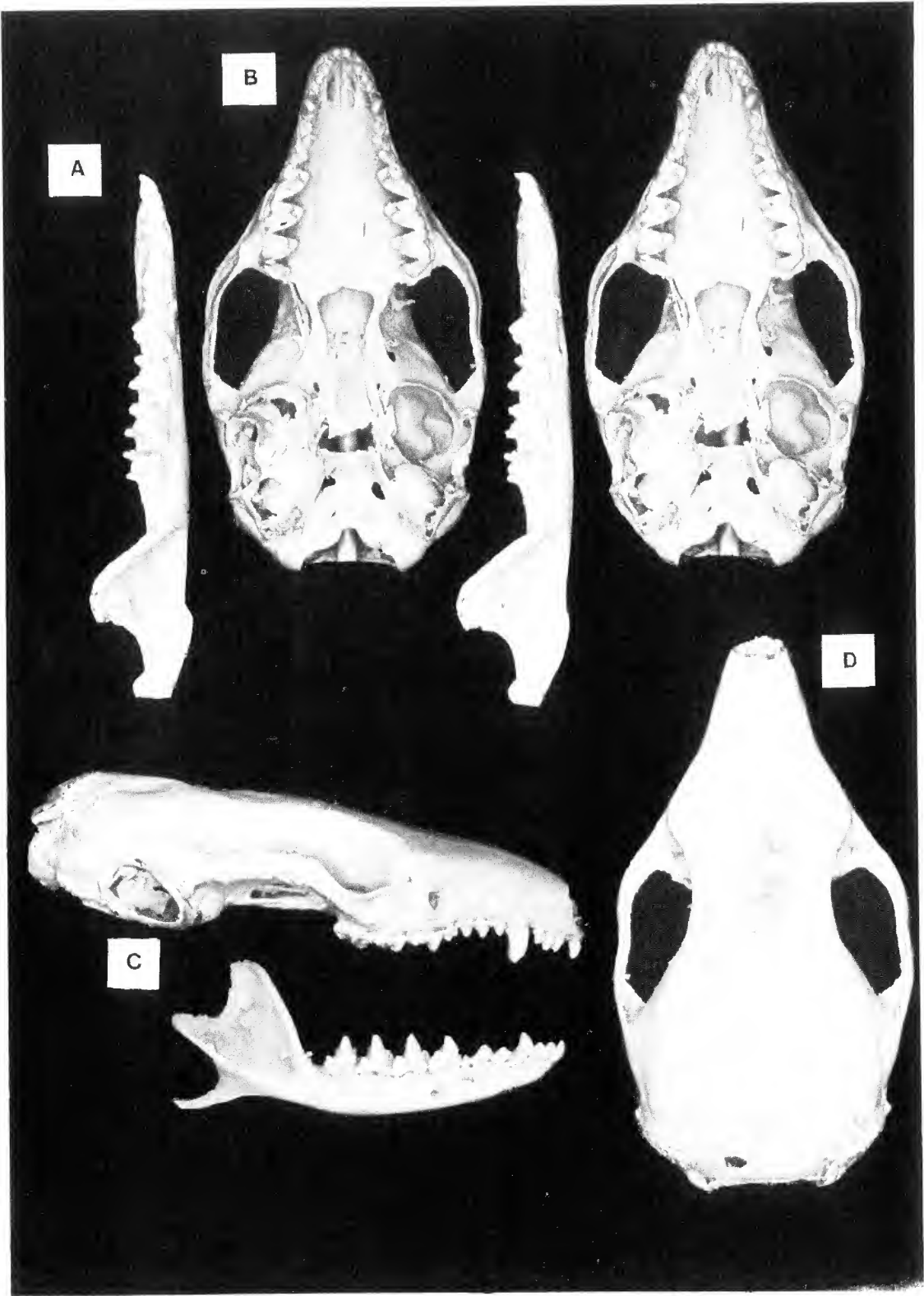


PLATE 48

A-D, *Planigale tenuirostris*, J3096, adult, Pittsworth, Qd. A,
× 6·2. B-D, × 4·1.

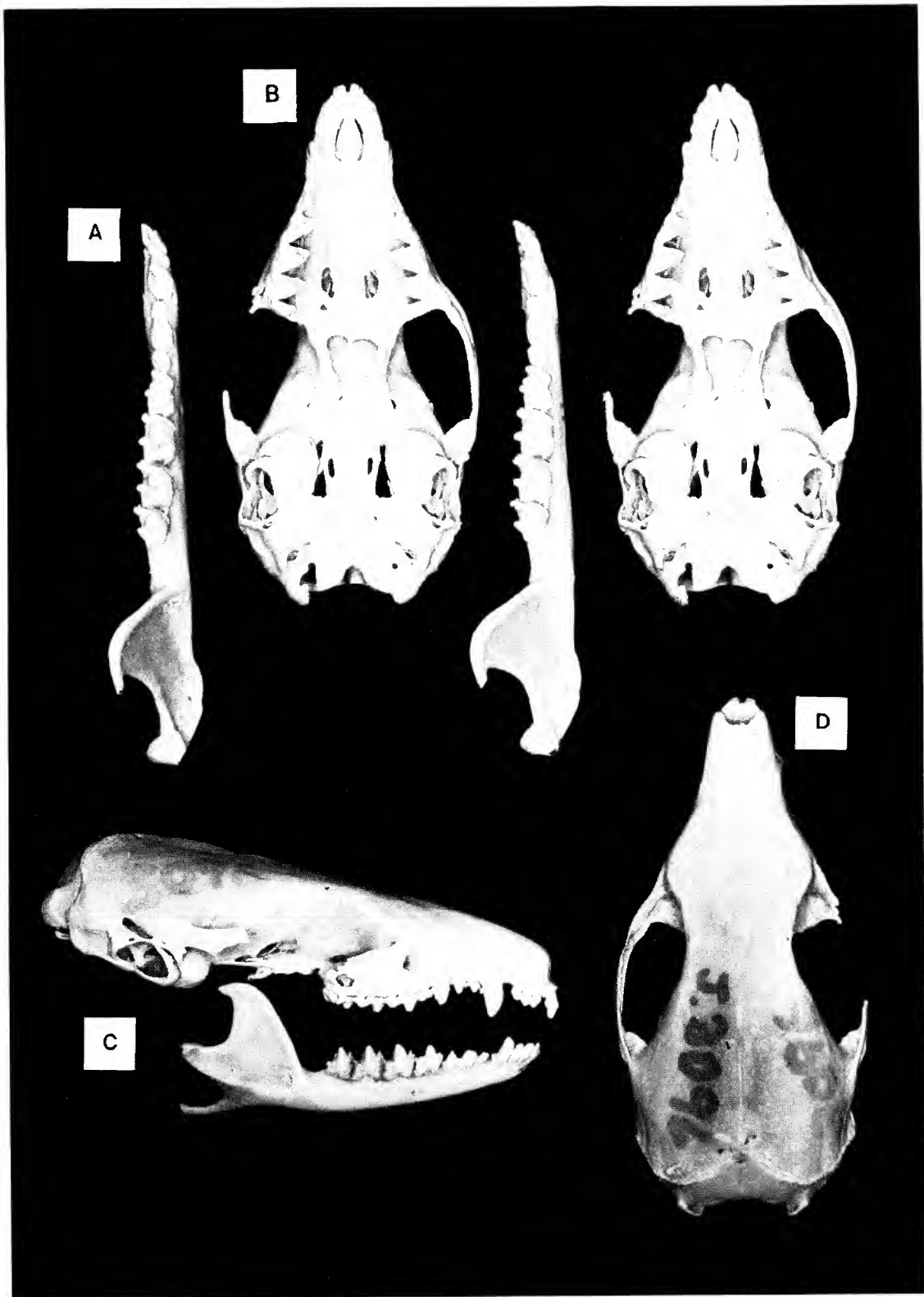


PLATE 49

A–D, *Planigale gilesi*. J21973, adult, Durrie Stn, nr Birdsville,
Qd. A, \times 5·9. B–D, \times 4·4.

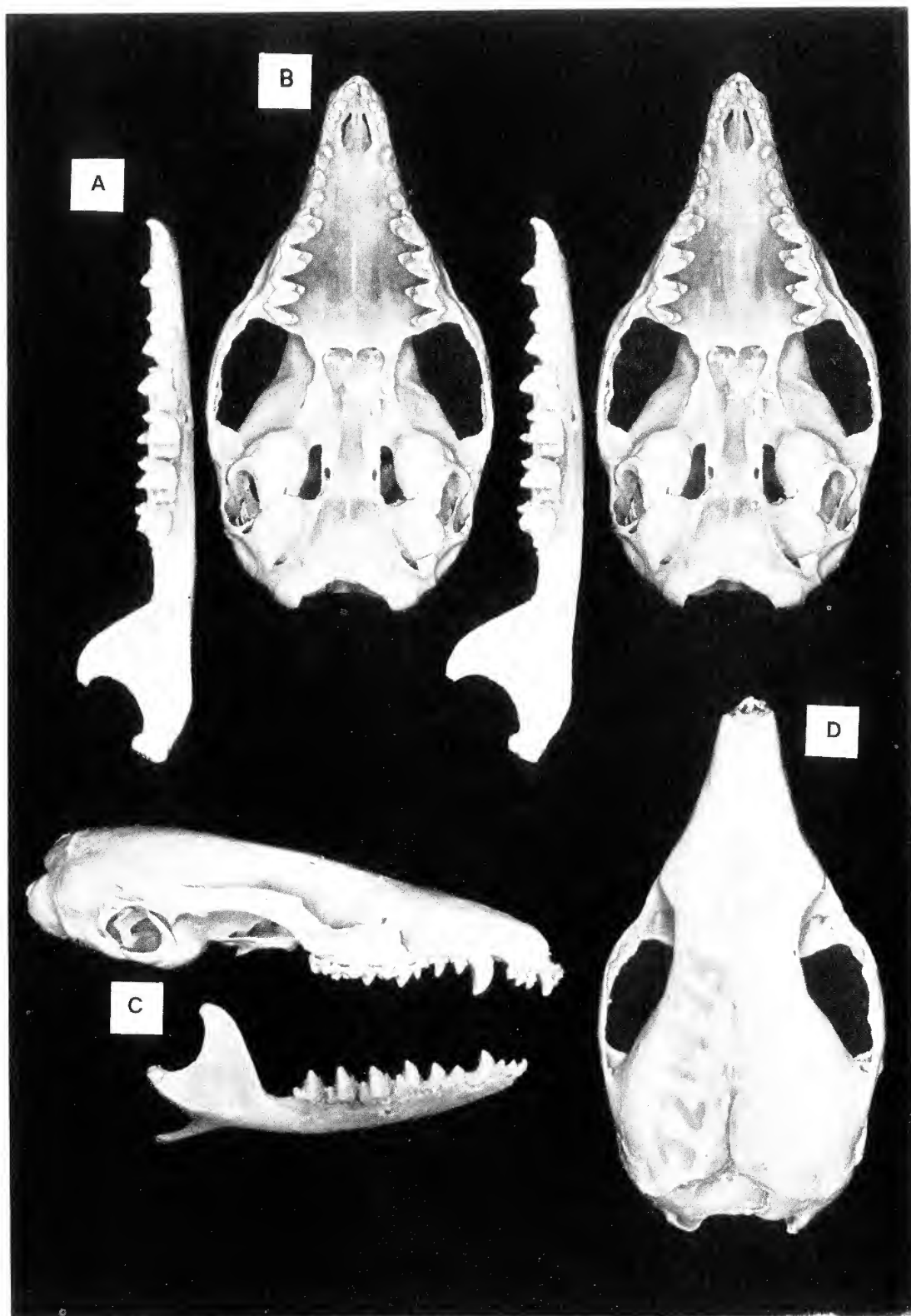


PLATE 50

A-D, *Planigale* sp. WAM M3432, adult, Tambrey, W.A. A,
× 5·6, B-D, × 4·0.

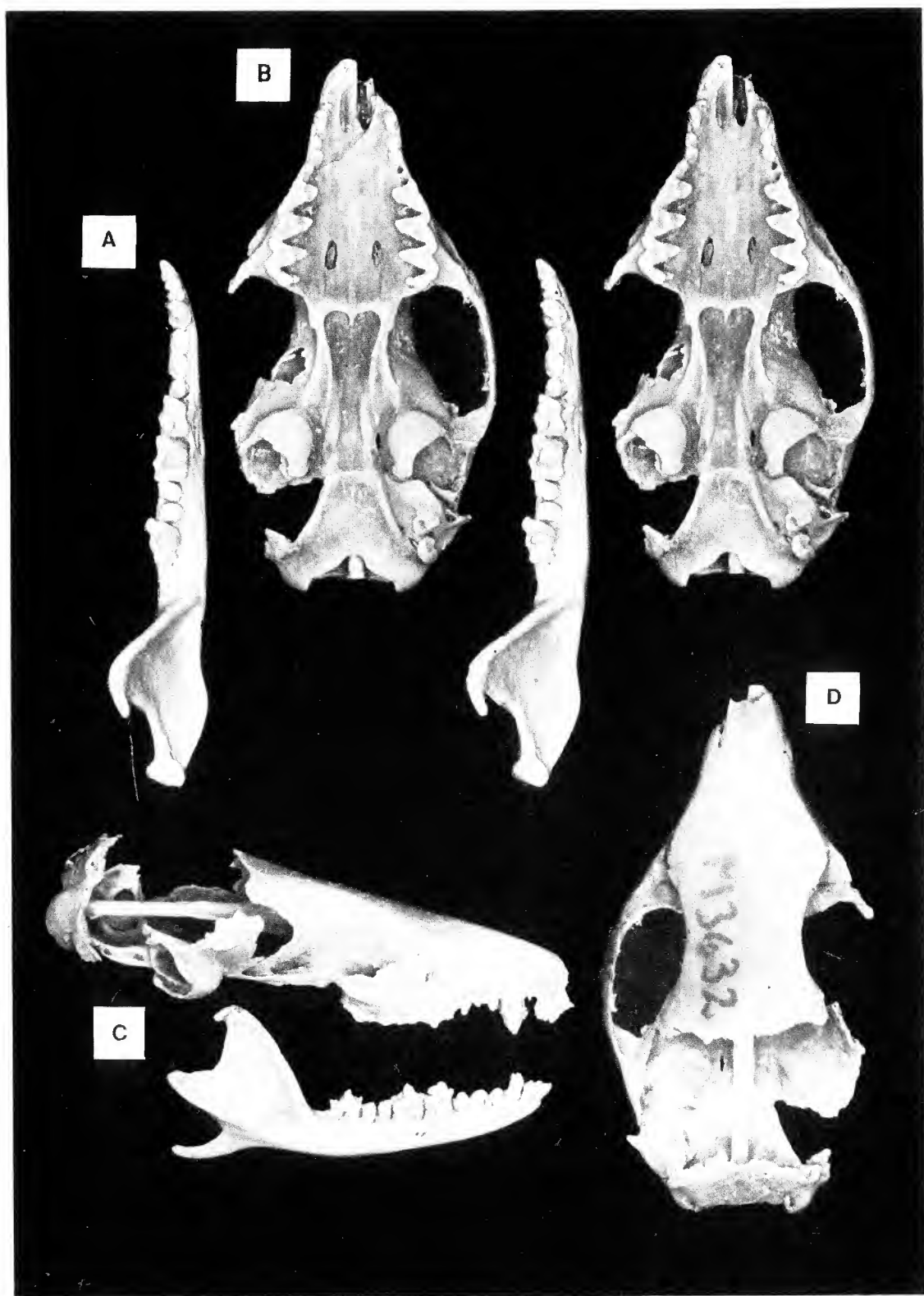


PLATE 51

A-B, *Planigale ingrami* (the *subtilissima* form), Ord River area, W.A. C-D, *Planigale maculata* (the typical form), Qd.

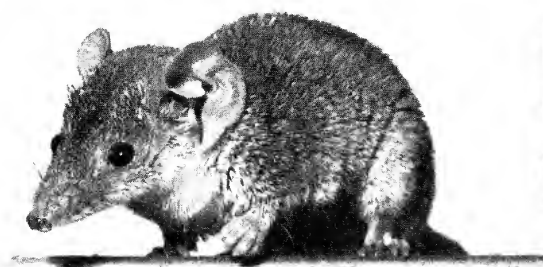
A



C



B



D





PHASCOLARCTID ORIGINS AND THE POTENTIAL OF THE SELENODONT MOLAR IN THE EVOLUTION OF DIPROTODONT MARSUPIALS

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ABSTRACT

Perameloids are regarded as ancestral to diprotodonts. Of known diprotodonts, the selenodont forms are structurally the best ancestors for the group. Dental and some cranial similarities between perameloids and selenodont diprotodonts are marked and indicate that bunodont diprotodonts such as burramyids are specialized derivatives of selenodont forms.

The majority of diprotodonts may be allocated into one of four groups based on dental morphology. Selenodont diprotodonts are probably monophyletic although two lineages can be recognized. Bunodont diprotodonts are almost certainly polyphyletic and contain forms with secondarily simplified molars. Ektopodont diprotodonts are monophyletic. Lophodont diprotodonts may be either polyphyletic or monophyletic.

Ektopodont diprotodonts have developed a type of lophodonty that is also partly developed in some phalangerids. This is achieved by a marshalling into rows of crenulations and conules. These transverse rows function as lophs and indicate one of perhaps three ways in which marsupial lophodonty could have been achieved.

It is commonly believed that bunodont burramyids such as *Cercartetus* are structurally the most primitive living diprotodonts (e.g. Tyndale-Biscoe 1973). *Phascolarctos* and other selenodont marsupials are regarded as specialized forms which probably evolved from ancestral bunodont diprotodonts. This view has been adopted in part because of the well-known secondary development of selenodonty in many eutherian groups (such as the origin of selenodont perissodactyls from bunodont condylarths) and in part because *Phascolarctos* and all other selenodont marsupials are assumed to be highly specialized leafeaters whereas bunodont diprotodonts are omnivores.

Recent basicranial (Archer 1976a) and dental investigations (Archer 1976b) of marsupicarnivores and perameloids have led to an alternative hypothesis presented here that selenodont diprotodonts evolved directly from perameloids and that they, not the bunodont diprotodonts, are structurally the most primitive.

The origin of marsupial lophodonty also requires new consideration in view of recently discovered Miocene diprotodonts. Ride (1971) has suggested an ingenious hypothesis for the origin of marsupial lophodonty which differs from the traditional view of Bensley (1903). The idea

presented below is yet a third way in which the evolution of lophodonty in marsupials may have occurred.

Terminology of teeth is shown in Plate 52 and follows in part that used by Archer (1975a, 1975b). Basicranial terminology is that given by Archer (1976a). Family names follow the usage of Kirsch (1968).

PERAMELOIDS AND THEIR RELATIONSHIP TO DIPROTODONTS

Ride (1964) divides Australian marsupials into three orders: Marsupicarnivora, including dasyurids and thylacinids; Peramelina, including only the superfamily Perameloidea which contains peramelids and thylacomyids; Diprotodonta, including all ten families of Australian diprotodonts.

Molars of perameloids differ from those of marsupicarnivores mainly in having a very large stylar cusp C which is subequal in size to stylar cusp D, and in lacking a crest which directly links the paracone and metacone. Lacking this crest, the posterior protocrista links with stylar cusp C and the anterior metacrista links with stylar cusp D, thereby providing a transverse valley through which the hypoconid passes from the protoconal

basin to the buccal side of the tooth. The lower molars of perameloids differ from those of most marsupicarnivores in having a relatively high talonid and, in all groups (but particularly so in thylacomyids), a reduced paraconid.

The ways in which perameloid molars differ from those of marsupicarnivores are also the ways in which they are similar to molars of selenodont diprotodonts. Winge (1941) believes that the phascolarctid molar is structurally primitive among diprotodonts. The phascolarctid upper molar may easily be seen as a slightly modified perameloid molar. The modifications required to transform the upper molars of *Perameles* (a structurally ancestral peramelid) into upper molars of phascolarctids would be a reduction in size of the styler cusps with approach of styler cusp C to styler cusp D, enlargement of the paracone and hypocone (the modified metaconule), greater development of the anterior and posterior cingula, and an increase in size of the metacone of M⁴. All of the principal shearing crests are comparable in the two groups. To similarly transform the lower molars, the perameloid paraconid must be reduced, the crista obliqua must intersect and connect to the paracristid, and the paracristid must not contact the tip of the metaconid.

Perameloids, like diprotodonts but unlike marsupicarnivores, are syndactylous. For this reason perameloids (although polyprotodont) are regarded by most authors (e.g. Osgood 1921, Ride 1964) as the group most likely to have been ancestral to diprotodonts. Opponents of this view must hold that syndactyly has developed at least twice, once in perameloids and at least once in diprotodonts (Thomas 1888, Kirsch 1968). There is no evidence for this (Jones 1924) and the only recent examination of syndactyly (Marshall 1972) has failed to provide reasons for regarding syndactyly to have evolved more than once. It is to be expected that if perameloids are ancestral to diprotodonts, traces of this ancestry might be evident in the teeth and basicrania of structurally ancestral diprotodonts.

STRUCTURALLY ANCESTRAL DIPROTODONTS

Burramyids include living forms which are generally regarded (e.g. Thomas 1888, Troughton 1967, Tyndale-Biscoe 1973) as most closely resembling hypothetical ancestral diprotodonts. These authors refer to similarity in molar morphology to some marsupicarnivores such as dasyurids and also to their low chromosome number. This similarity consists of the subtriangular shape of the burramyid upper molar which lacks or has

only a poorly-defined hypocone. Bensley (1903) regards these forms as indicative of an intermediate condition between ancestral tribosphenic marsupials which lack the hypocone and more advanced phalangerids which have well-developed hypocones. If burramyids are ancestral to phascolarctids, the latter must have redeveloped a complete styler shelf as well as a majority of the shearing crests which, although absent in burramyids, are present in perameloids and marsupicarnivores. Alternatively, the burramyid condition could be a simplification of a more complex morphology such as that of phascolarctids and some petaurids, a view held by Winge (1941) and accepted here.

Of all 'possum' groups (phalangerids in the sense of Ride 1964; there is no corresponding taxon in the more recent classification of Kirsch 1968) the closely related phascolarctids and vombatids are also the only ones to have a variably developed alisphenoid-frontal contact on the side of the braincase, a feature found in all perameloids (Archer 1975b summarizes the distribution of this character in marsupials). Further, the 2N chromosome number of perameloids (not including thylacomyids) and vombatids is 14, and of phascolarctids 16, 14 being regarded as structurally primitive among marsupials (Sharman 1974). Serologically (Kirsch 1967, 1968), phascolarctids and vombatids are closely related, but perameloids group with dasyurids. However, the serological distance between phascolarctids and perameloids may be the result of relatively rapid protein evolution in phascolarctids (and vombatids).

At present, available evidence suggests phascolarctids (and possibly other selenodont forms) are the group best regarded as structurally ancestral to other diprotodonts.

DIVERSITY OF MOLAR PATTERNS AMONG DIPROTODONTS

With the exception of *Tarsipes* whose dental morphology is deceptively simple, presumably the result of degeneration from a more complex ancestral pattern, all diprotodont molars may be categorized as being either selenodont, bunodont, lophodont, or what may be referred to as ektopodont. With the exception of the ektopodont pattern (Plate 52), these types are figured by Bensley (1903).

SELENODONT DIPROTODONTS: Selenodont forms include all phascolarctids (*Phascolarctos*, *Perikoala*, *Pseudokoala*, *Litokoala*) some petaurids (*Pseudocheirus*, *Hemibelideus*, and *Schoinobates*) and possibly vombatids (*Vombatus*, *Lasiiorhinus*, *Phascolonus*, *Rhizophascolonus*) to judge from

unworn teeth. It has been suggested (e.g. by Kirsch 1968) that phascolarctids and selenodont petaurids represent separate lineages, the development of selenodonta in the two lineages possibly being the result of convergence. Bensley (1903), and Turnbull and Lundelius (1970) point out significant differences in molar form in the two groups. However, it is also possible that the two groups had a common selenodont ancestor, differences noted in the modern representatives being nothing more than specialization developed later by each group. Bensley (1903) regards the *Phascolarctos* molar pattern as a derivative of the *Pseudocheirus* condition, while Winge (1941) interprets a structural trend which goes from *Phascolarctos* to *Pseudocheirus*. Kirsch (1967, 1968) has shown that serologically *Phascolarctos* groups with vombatids rather than the other selenodont forms which group with the remaining diprotodonts. If phascolarctids (and vombatids) have undergone rapid protein evolution relative to other diprotodonts, their serological uniqueness could obscure relationships that may exist with other selenodont diprotodonts. Sharman (1974) notes that because *Phascolarctos* has $2N=16$ chromosomes, it is closer to the assumed primitive number of 14, and differs from other selenodont diprotodonts which range from 20 to 22. The significance of this is difficult to interpret in view of the fact that within one family (the macropodids), the range is 10 to 32.

In view of the generally held notion (Troughton 1967, Ride 1970) that selenodont diprotodonts are strictly herbivorous, it seems appropriate to point out here that Common Ringtails (*Pseudocheirus peregrinus*) held in captivity by the author invariably show a decided preference for insects if given a choice between these and any type of leaf or fruit.

BUNODONT DIPROTODONTS: Bunodont forms include some petaurids (*Petaurus*, *Gymnobelideus*, and *Dactylopsila*), burramyids (*Acrobates*, *Distoechurus*, *Cercartetus*, and *Burramys*), phalangerids (*Trichosurus*, *Wyulda*, and *Phalanger*), potoroine macropodids (*Hypsiprinodon*, *Bettongia*, *Caloprymnus*, *Aepyprymnus*, *Potorous*, and *Propleopus*), and thylacoleonids (*Thylacoleo* and *Wakaleo*). Bensley (1903) regards the more tritubercular forms such as *Distoechurus* to be structurally ancestral to other bunodont diprotodonts, considering the absence of a hypocone to be structurally primitive. He also suggests that bunodont and selenodont forms may have been independently derived from tritubercular (Bensley's hypothetical properamelid) ancestors. This seems doubtful considering that selenodont and bunodont dipro-

todonts have many characters in common such as diprotodonty, reduced upper incisor number, wrinkled enamel, fasciculus aberrans, serological characters, and highly modified basicranium involving fusion of the ectotympanic (although fusion does not occur in some *Phascolarctos*) which are not present in known tritubercular groups. It seems more reasonable to regard selenodont and bunodont diprotodonts as having been derived either from one another or from other diprotodont ancestors, rather than independently derived from tritubercular ancestors. Winge's (1941) view, that bunodont forms were derived from selenodont forms, is accepted here because of the presence of traces of selenodonta and the common occurrence of wrinkled enamel in bunodont diprotodonts. This interpretation implies that the more tritubercular and less selenodont forms such as *Distoechurus* are in fact highly specialized forms, and not, as Bensley (1903) believes, structurally primitive.

The unity of the bunodont diprotodonts is very doubtful and several independent origins, possibly from selenodont forms of different sorts, are probable. Bunodont non-macropodids have a $2N$ chromosome number of 14 to 20 (Sharman 1974). *Phalanger*, regarded here as a structurally primitive bunodont form, has 14 but so do burramyines which are regarded here as structurally advanced. Kirsch (1967, 1968) also regards the bunodont forms to represent several distinct serological groups.

EKTOPODONT DIPROTODONTS: Ektopodont forms are represented by the late Miocene species *Ektopodon serratus* (Stirton, Tedford and Woodburne 1967). They are characterized in part by transverse serrate ridges formed by numerous small upside down V-shaped longitudinal crests. *Ektopodon* was originally described as a possible monotreme, but Woodburne (pers. comm.) suggests it is a diprotodont following the discovery of an older and simpler species.

LOPHODONT DIPROTODONTS: Lophodont forms include macropodine macropodids and diprotodontids. Traditional views of the origin of lophodonta from bunodonta (such as proposed by Bensley 1903) involve evolution of crests or lophs which link the protocone to the paracone and the hypocone to the metacone. In lower molars it is generally assumed that the paracristid and paraconid become reduced, the metacristid develops as the anterior lophid, and the hypocristid develops as the posterior lophid. The crista obliqua becomes the midlink of macropodines.

The importance of *Ektopodon* in the present context is that it demonstrates that diprotodont lophs may not be homologues of the crests of other marsupials. Thomas (1888, p. 193) notes that in some species of *Phalanger* the molars have distinct transverse ridges. These transverse ridges could be regarded as incipient lophs. Close inspection of unworn molars reveals a striking similarity to molars of *Ektopodon*. The buccal half of the transverse ridges of upper molars and the lingual half of the ridges of lower molars appear to consist of numerous upside-down V-shaped longitudinal crests. The lingual half of the transverse ridges of upper, and the buccal end of the transverse ridges of lower molars consist of short steep-sided ridges which appear to be the homologues of ridges in these positions of molars of *Phascolarctos*. The remainder of the crown surface of *Phalanger* molars are covered in small wrinkles and crenulations, as are the teeth of selenodont and many bunodont diprotodonts. This suggests the possibility that lophs may have evolved through a marshalling together of wrinkles, conules and small ridges already present in ancestral selenodont

forms. Overriding this organization in *Phalanger*, as in most bunodont forms, are the remnants of selenodont crests, now modified to form triangular buttresses at the ends of transverse lophs. This transformation is as readily performed on lower as it is on upper molars.

In completely lophodont forms, the lophs are not clearly modified ancestral ridges. It is possible that marsupial lophodonty evolved more than once and in very different ways. Ride's (1971) interesting hypothesis for origin of macropodine molars assumes that a tritubercular pattern was ancestral to the lophodont pattern, that styler cusps became the buccal ends of the upper lophs, and the paracone and metacone were incorporated along the length of the lophs. An alternative is that the lophodont molar has been derived from a selenodont molar in the manner outlined above. Lateral selenes became triangular buttresses (homologues of which occur in many macropodids), and transverse lophs were formed by a marshalling of conules, ridges and wrinkles. The already well-developed hypocones, reduced paraconids, and enlarged M4 of selenodont forms could have been characters directly utilized by ancestral lophodont forms. If this latter hypothesis for the origin of lophodonty is accepted, bunodont potoroine macropodids could be regarded as derivatives of lophodont macropodines, a conclusion also accepted by Ride (1971).

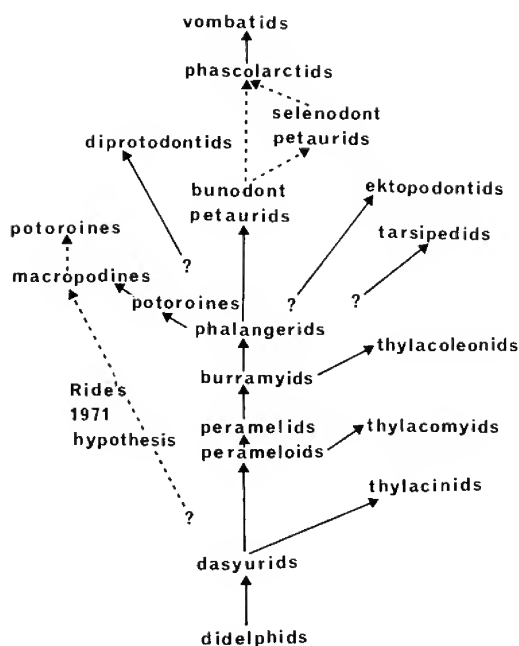


FIG. 1: Some traditional concepts of origins for Australian marsupial families. The two macropodid sub-families are treated separately. These concepts are based largely on Bensley (1903) with modifications suggested by later authors. Wynyardiids are not shown because their teeth are unknown. Dashed lines indicate alternative origins, such as Ride's (1971) hypothesis for the origin of macropodids.

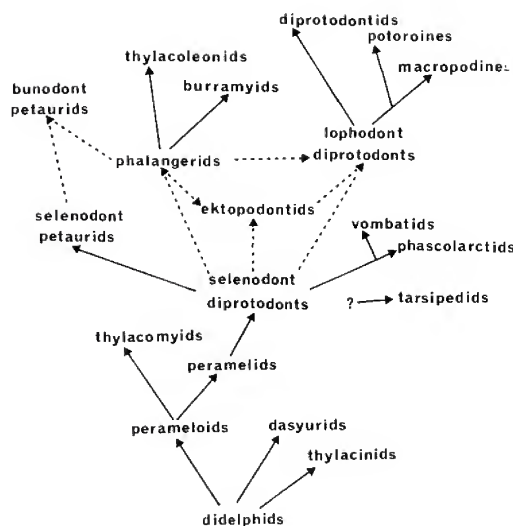


FIG. 2: Concepts of origin suggested in the present work. Alternatives are indicated by dashed lines.

CONCLUSIONS

Various views of descent noted above are contrasted in Figs. 1–2. It is suggested here (as shown in Fig. 2) that selenodont diprotodonts arose directly from peramelids and were the base stock for all other diprotodont radiations.

The relationship between ektopodontids and other diprotodonts is unclear. They exhibit a transverse lophodont molar pattern which, although possibly convergent on other lophodont forms and derived from phalangerids, indicates a unique way in which lophodonty could be developed from selenodonty.

It is not clear how lophodonty was achieved in macropodids or diprotodontids. It could have developed from either the bunodont, ektopodont, or selenodont pattern. Ride (1971) suggests the additional possibility that lophodonty developed as a modification of a more or less tribosphenic pattern.

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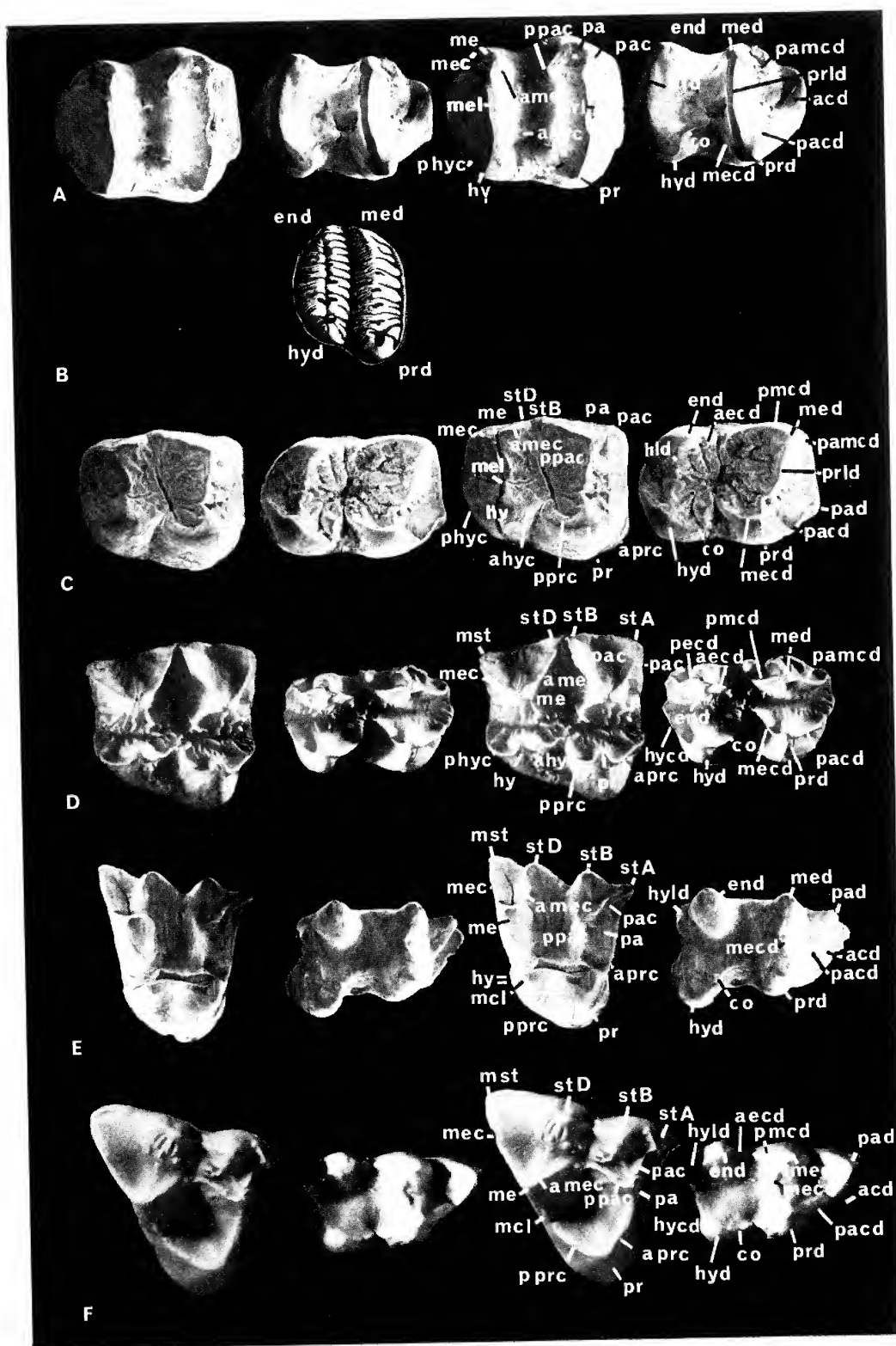
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PLATE 52

- A. *Dendrolagus humholtzi*, a lophodont macropodid. RM^2 ($\times 4.5$) and RM_2 ($\times 4.5$) scanning electron microscope stereophotographs.
- B. *Ectopodon serratus*, an ectopodontid. Shown as ? RM^x (reversed and modified from Fig. 7 of Stirton, Tedford and Woodburne 1967).
- C. *Phalanger nudicaudatus*, a bunodont phalangerid. RM^2 ($\times 4.1$) and RM_2 ($\times 4.2$) scanning electron microscope stereophotographs.
- D. *Phascolarctos cinereus*, a selenodont phascolarctid. RM^2 ($\times 3.1$) and RM_2 ($\times 3.2$) stereophotographs.
- E. *Perameles bougainville*, a tribosphenic peramelid. RM^2 ($\times 7.9$) and RM_2 ($\times 8.1$), scanning electron microscope stereophotographs.
- F. *Didelphis virginiana*, a tribosphenic didelphid. RM^2 ($\times 4.1$) and RM_2 ($\times 3.8$), stereophotographs.

Abbreviations: *acd*, anterior cingulid; *aecd*, anterior entocristid; *ahyc*, anterior hypocrista; *amec*, anterior metacrista; *aprc*, anterior protoecrista; *co*, crista obliqua; *end*, entoconid; *hld*, hypolophid; *hy*, hypocone; *hyed*, hypocristid; *hyd*, hypoconid; *hyld*, hypoconulid; *mcl*, metaconule; *me*, metacone; *mec*, metacrista; *mecl*, metacristid; *med*, metaconid; *mel*, metaloph; *mst*, metastylar corner of tooth; *pa*, paracone; *pac*, paracrista; *pacd*, paracristid; *pamed*, para-metacristid; *pecd*, posterior entocristid; *phyc*, posterior hypocrista; *pmcd*, posterior metacristid; *pprc*, posterior protoecrista; *pr*, protocone; *prl*, protoconid; *prld*, protoloph; *prld*, protolophid.





THE GENUS *WALLABIA* TROUESSART (MARSUPIALIA: MACROPODIDAE) IN THE UPPER CAINOZOIC DEPOSITS OF QUEENSLAND

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ABSTRACT

The previously monotypic genus *Wallabia* Trouessart, 1905, is re-defined to include a fossil species, *W. indra* (De Vis, 1895) from the Upper Cainozoic fluvial deposits of the Darling Downs area, southeastern Queensland. '*Halmaturus*' *vishnu* De Vis, 1895, is shown to be synonymous with *W. indra*.

The present study comprises part of an overall revision of the fossil macropodids from the Pleistocene fluvial deposits in the eastern Darling Downs and the Chinchilla Sand of Late Pliocene age in the west of this area. The majority of the larger grazing macropodines were referred by De Vis (1895) to *Halmaturus* Illiger, a junior secondary synonym of *Macropus* Shaw. Bartholomai (1967, 1973a, 1973b, 1975) has shown that the material included representatives of the genera *Troposodon* Bartholomai, 1967, *Protemnodon* Owen, 1874, *Fissuridon* Bartholomai, 1973 and *Macropus* Shaw, 1790, in addition to material which is here referred to *Wallabia*. This material is relatively uncommon compared with other large grazing elements in the faunas represented, and the available sample is too small to permit statistical evaluation of the population from which it was drawn.

All measurements throughout are in millimetres.

Genus *Wallabia* Trouessart, 1905

Wallabia Trouessart, 1905, p. 834 (type species *Kangurus bicolor* Desmarest, 1804 = *Kangurus ualabatus* Lesson, 1827, by subsequent designation of Iredale and Troughton, 1934).

In addition to designating *Wallabia bicolor* (Desmarest) as the type species for the genus *Wallabia*, Iredale and Troughton (1934) followed Trouessart (1905) in listing all of the extant, medium-sized brush wallabies within this genus. These species previously were regarded mainly within the genus *Macropus*. No attempt was made to take into account any related fossil species, but later, Troughton (1937, 1957) indicated the generic

distinctness of species now referred to *Protemnodon* by Bartholomai (1973a). Troughton presented no convincing arguments to support this separation. Tate (1948) used *Protemnodon* widely for both living and fossil wallabies, while Stirton (1963) separated living and fossil representatives, using *Wallabia* for living species and *Protemnodon* for extinct forms.

Bartholomai (1973a, 1975) has introduced cranial morphological differences, results of comparative reproductive physiological studies by Sharman *et al.* (1966) and chromosome studies by Sharman (1961) to indicate the distinctness of *Wallabia bicolor*, the only living species referred to the genus, from all other living wallabies. Research by Kirsch (1968) on marsupial haemoglobin suggests that the species of wallabies and kangaroos, including *W. bicolor*, *Megaleia* and *Lagorchestes* are closely associated, but Bartholomai (1975) indicates that this cannot be verified from the fossil record because of general deficiencies in the known fossil samples available.

Calaby (1966) concludes, on the basis of behaviour and distinctive dental characters, that *Wallabia* should be recognized as a monotypic genus. This conclusion is supported here for living forms. Only a single species is added from the known fossil record.

GENERIC DIAGNOSIS: Medium sized macropodids; cranium with rostrum little deflected; diastema short; premaxillae relatively narrow in occlusal view; infraorbital canal very short; foramen ovale open, less anterolaterally directed than in *Macropus*; additional foramina usually present in alisphenoid bulla, lateral to, connected but well

separated from foramen ovale, presumably for mandibular branch of trigeminal nerve; basioccipital very broad between petrosals; anterior margin of basioccipital with reduced elevation; basisphenoid slope low; dorsal margin of supraoccipital narrowly U-shaped. Palate shallowly excavate and slightly downturned posteriorly. Masseteric foramen almost below anterior cheek teeth. I^3 groove at posterior one-third of lateral surface; DP^3 and anterior upper molars with strong ridges from paracone and metacone uniting across median valley; forelink absent. Lower molars with relatively low, rectilinear lophids and links; lateral margins of lophids bulbous; posterior surface of hypolophid not ornamented.

***Wallabia indra* (De Vis, 1895)**

(Plate 53, Figs. 1–6)

Halmaturus indra De Vis, 1895, pp. 112–3, pl. 17, figs. 18, 20.

Halmaturus vishnu De Vis, 1895, pp. 114–6, pl. 17, figs. 3–4.

'*Halmaturus*' *vishnu* De Vis: Stirton, 1959, p. 124; Bartholomai, 1966, pp. 121–2, pl. 16, figs. 1–3.

'*Halmaturus*' *indra* De Vis: Bartholomai, 1966, pp. 116–7, pl. 15, figs. 4–6.

MATERIAL: Holotype, F3595, partial left mandibular ramus with P_2 – M_1 (unerrupted P_3 removed by fenestration, and no longer in the Queensland Museum collections), Darling Downs, SE.Q., (figd in part, De Vis, 1895, pl. 17, figs. 18, 20; figd Bartholomai, 1966, pl. 15, figs. 4–6). Preservation suggests derivation from the Chinchilla Sand, of Late Pliocene age.

Also referred is the lectotype of '*Halmaturus*' *vishnu*, F3860, a partial left mandibular ramus with P_3 – M_4 , adult, Darling Downs, SE.Q., (figd in part, De Vis, 1895, pl. 17, figs. 3–4; figd Bartholomai, 1966, pl. 16, figs. 1–3). Preservation suggests derivation from the Pleistocene fluviatile deposits of the eastern Darling Downs.

In addition, 7 juvenile mandibular rami, 8 adult mandibular rami and one maxillary fragment are referred from the following localities in the Darling Downs: Chinchilla; Middle Gully System, Chinchilla Rifle Range (Rifle Range No. 78, Par. Chinchilla); Dalby at 34–35 feet (c. 11 m) in a pump well; and from the eastern and western Darling Downs (particular localities unspecified).

SPECIFIC DIAGNOSIS: A relatively large species, with mandibular symphysis very slightly elevated, and with diastema relatively short. Lower cheek teeth low; P_2 with only one set of vertical labial and lingual ridges transecting crest; P_3 approximately as long as M_4 , the longest molar; longitudinal crest nearly straight; anteriorly, base markedly tumescent; crest transected by 3–4 sets of ridges. DP_3 protolophid very narrow at crest, rectilinear, with forelink descending directly from protoconid; labial moiety of trigonid basin much reduced.

Lower molars relatively broad with lophid margins broadly curved from crown base to crests in anterior view; lophid crests somewhat rectilinear; midlink moderately poorly developed; posterior cingulum absent. Upper molars relatively low, with strong anterior ridge from paracone, broad anterior cingulum, and posterior ridges from metacone and hypocone of similar strength, uniting well above crown base, delimiting slight posterior fossette.

DESCRIPTION: Mandible narrow, rather shallow. Symphysis not ankylosed, set at very low angle to base of mandible. Diastema relatively short, geniohyal pit very shallow, below anterior margin of P_3 . Ventral margin of ramus rounded. Mental foramen moderately large, oval, well anterior to P_3 , and just below diastemal crest. Ramus with shallow labial groove from below P_3 extending posteriorly to below M_2 and occasionally to below centre of M_3 . Lingually, broad depression leads posteriorly to pterygoid fossa. Post-alveolar shelf short, leading to mesial wall of coronoid process. Masseteric crest raised to below level of alveolar margin. Angle of mandible, condyle and bulk of coronoid process not preserved.

I_1 unknown.

P_2 relatively short, robust, subovate in basal outline; longitudinal crest secant, curving slightly lingually in its posterior extension; transected mesially by a single set of vertical labial and lingual ridges, with production of well defined cuspule at crest; crown basally with labial and lingual tumescences, continuous around anterior margin, with production of small anterior basal cuspule.

DP_3 molariform, subtriangular in basal outline; lophids moderately low, with hypolophid crest much broader than protolophid; protolophid rectilinear but with hypolophid somewhat convex posteriorly; protoconid positioned above crown axis. Trigonid basin narrow, extremely poorly developed labially, short, its length being much less than distance between lophids. Forelink high, strong, descending without curvature anteriorly to point labiad to mid-point of high anterior cingulum, occasionally ornamented labially and lingually by a set of weak accessory ridges; antero-lingual fossette developed in trigonid basin in conjunction with slight, variable anterior ridge from metaconid. Posterior ridge from protoconid moderately strong, curving labially to unite with moderately strong midlink, curving antero-lingually from hypoconid; posterior ridge from metaconid weak, descending into lingual extremity of rounded talonid basin; labial moiety of talonid poorly developed descending at high angle from

TABLE 1: MEASUREMENTS FOR *Wallabia indra* (DE VIS), MANDIBLE

Specimen	P ₂	DP ₃	P ₃	M ₁	M ₂	M ₃	M ₄
F3595*	6.7 × 4.3	7.1 × 4.2	—	8.5 × 5.6	—	—	—
F3860	—	—	10.1 × 4.1	7.8 × —	9.4 × 6.5	10.4 × 7.5	10.7 × 7.3
F4743	—	—	— × 4.7	7.6 × 5.7	9.0 × —	10.6 × 7.6	11.2 × 7.5
F4741	—	—	10.3 × 4.1	7.5 × —	8.5 × —	10.0 × —	10.8 × 7.0
F4746	—	—	—	—	8.7 × 5.7	9.8 × 6.8	10.0 × 6.8
F4749	—	6.7 × 3.4	—	— × 4.9	—	—	—
F4742	—	—	—	—	—	9.8 × 7.3	10.4 × 7.2
F4747	—	—	—	—	8.5 × 6.0	10.0 × 7.2	10.8 × 7.5
F3597	—	—	—	—	8.8 × 6.1	10.7 × 7.4	10.8 × 7.5
F2496	—	—	—	7.3 × 4.8	8.3 × 5.6	9.8 × 6.2	—
F4753	—	—	—	8.0 × 5.7	8.9 × 6.5	—	—
F4751	—	—	—	7.5 × 5.1	8.7 × 6.1	—	—
F4752	—	—	—	8.1 × 4.9	9.1 × 5.9	—	—
F4744	—	—	—	—	9.0 × 6.2	9.6 × 6.9	—
F3601	—	—	—	8.1 × 5.1	8.5 × 6.1	8.5 × 6.1	—

*Holotype

midlink. Anterior ridge from entoconid weak. Posterior of hypolophid rounded, unornamented, occasionally with slight posterolabial basal swelling.

P₃ elongate, subovate in basal outline, only very slightly shorter than M₄. Longitudinal crest secant, extremely slightly concave labially, or straight, transected by three or four sets of vertical labial and lingual ridges, with production of cuspules at crest; strength of ridges decreases posteriorly; base of crown markedly tumescent, produced to form noticeable cingulum anteriorly.

M₁ < M₂ < M₃ < M₄; molars subrectangular in basal outline, slightly constricted across talonid basin in anterior molars, more strongly constricted in posterior molars; lophids relatively low, almost rectilinear, with hypolophid somewhat more convex posteriorly; protolophid narrower than hypolophid in M₁ and M₂, but broader in M₃ and much broader in M₄; lateral surfaces of lophids markedly convex. Trigonid basin usually very broad, its length almost equalling distance between lophids. Forelink low, moderately strong, unornamented, descending anterolingually from protoconid, across labial moiety of trigonid basin, usually uniting with low anterior cingulum, labiad to axis of crown; very weak accessory ridge descends anteriorly from metaconid towards trigonid basin; lingual position of trigonid near horizontal, labial portion reduced and sloping. Slight ridge descends posteriorly from metaconid, occasionally uniting with similar ridge from entoconid across lingual margin of talonid basin. Midlink from hypoconid low, crossing labial

moiety of talonid basin to unite with slight ridge from protolophid, labiad to axis of crown. Posterior of hypolophid unornamented, occasionally with swollen base delimited as slight posterior cingulum.

TABLE 2: MEASUREMENTS FOR *Wallabia indra* (DE VIS), MAXILLA

Specimen	M ²	M ³	M ⁴
F4740	8.6 × 7.4	9.6 × 7.7	9.7 × 7.2

Upper incisors, P², DP³, P³ and M¹ unknown.

M² < M³ < M⁴; molars subrectangular in basal outline, somewhat constricted across median valley. Lophs low, with protoloph slightly narrower than metaloph in M² and somewhat broader in M³ and M⁴, slightly anteriorly curved. Anterior cingulum relatively low, labially subhorizontal, but linguallly ascending slightly, short; forelink not well defined, but anterior ridge from paracone strong, ascending slightly linguallly to labial margin of cingulum. Posterior ridge from paracone weak, ascending into median valley. Midlink low, weak, curving posterolinguallly across median valley to unite with slight ridge from near mid-point of metaloph; lingual moiety of median valley V-shaped, labial moiety sharply U-shaped; low ridge occasionally present across lingual extremity of valley. Posterior ridges from metacone and hypocone moderately strong, approximately equally developed, uniting to delimit slight posterior fossette below axis of crown. Base of crown somewhat swollen posteriorly and posterolinguallly.

DISCUSSION: Bartholomai (1966) redescribed and refigured the holotype specimen of *Wallabia indra* (De Vis), the only specimen referred by De Vis (1895) to the species. In the same publication, Bartholomai (1966) selected F3860 as the lectotype of '*Halmaturus*' *vishnu* De Vis. The holotype specimen of *W. indra* has preservation suggesting its derivation from the Chinchilla Sand of Late Pliocene age, while the lectotype of '*H*' *vishnu* appears to have been collected from Pleistocene fluvial deposits of the eastern Darling Downs. The specimens are not accompanied by accurate locality data, but material here referred to *W. indra* has been derived from both deposits.

Neither the holotype of *W. indra* nor the lectotype of '*H*' *vishnu* is figured herein, as adequate illustrations are presented in Bartholomai (1966 pl. 15, figs. 4–6, and pl. 16, figs. 1–3, respectively).

Although the samples from these areas are small, sufficient evidence exists to indicate almost complete overlap in size, and mandibular measurements are presented in Table 1. Morphologically, no differences are apparent in the material at present known, and relegation of '*H*' *vishnu* to synonymy is considered justifiable. It should be noted, however, that the complete dentition of the species is as yet unknown. The single referred maxilla, measurements for which are provided in Table 2, is from the Chinchilla Sand, at Chinchilla.

It is usual for material from the eastern Darling Downs to be specifically distinct from that in the

Chinchilla Sand, but as indicated for the genus *Troposodon* by Bartholomai (1967), this is not without exception. Geologically, the time difference between the Chinchilla Sand and the Pleistocene fluvial deposits does not appear to be excessive and the occasional occurrence of the same species in both stratigraphic units is not surprising.

Association of upper and lower jaw fragments has been effected by considerations of both size and morphology, and while fragments have not, as yet, been located together, their present association is considered correct. No post-cranial remains have been referred to *W. indra* although considerable disarticulated material, derived from small macropodine species, is present in the collections of the Queensland Museum.

Remarkable morphological similarity exists between *W. indra* and the extant *W. bicolor* (Desmarest), the type species of the genus. Indeed, the only distinction which can be drawn at this stage is in regard to the sizes of the species involved. While it has been shown by Bartholomai (1975), with respect to *M. agilis siva* (De Vis), that size differences may be generally insufficient for even subspecific distinction, the *W. indra* sample is too small to enable statistical evaluation to be undertaken at this stage. The log difference diagram shown in Fig. 1, is based on single specimens, but nevertheless illustrates the similarity in proportions existing in the cheek teeth of *W. indra* and *W. bicolor*. The similarly elongate nature of P_3 compared with the molars is particularly evident.

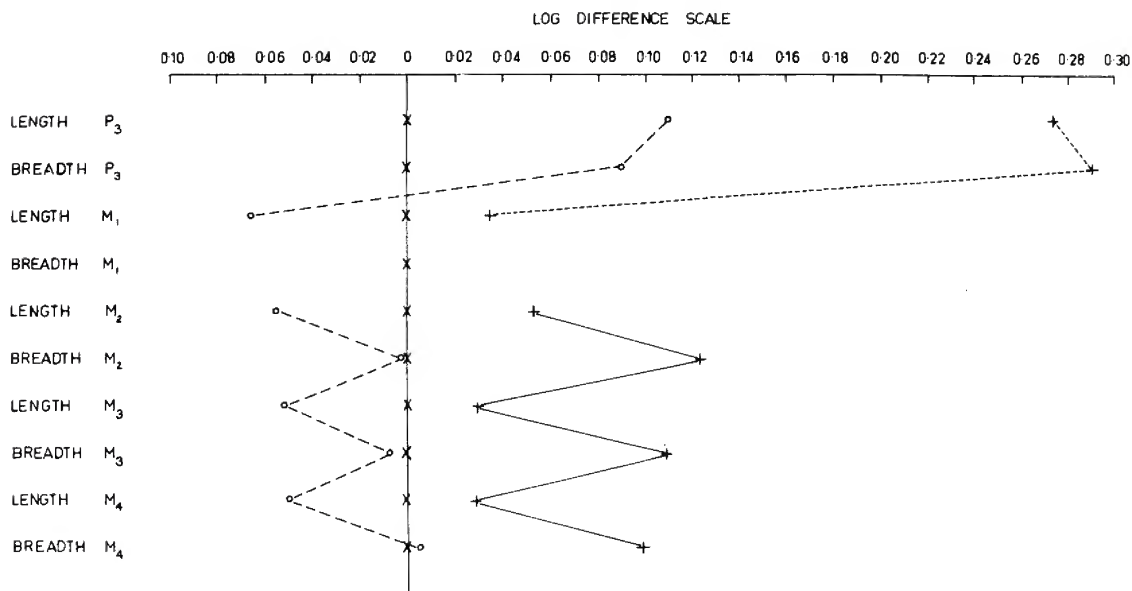


FIG. 1: Log difference diagram illustrating proportional relationships of *Wallabia indra* (F3860, ♀) and *W. bicolor* (J4890, ♂), using *Macropus parryi* (J10756) as standard.

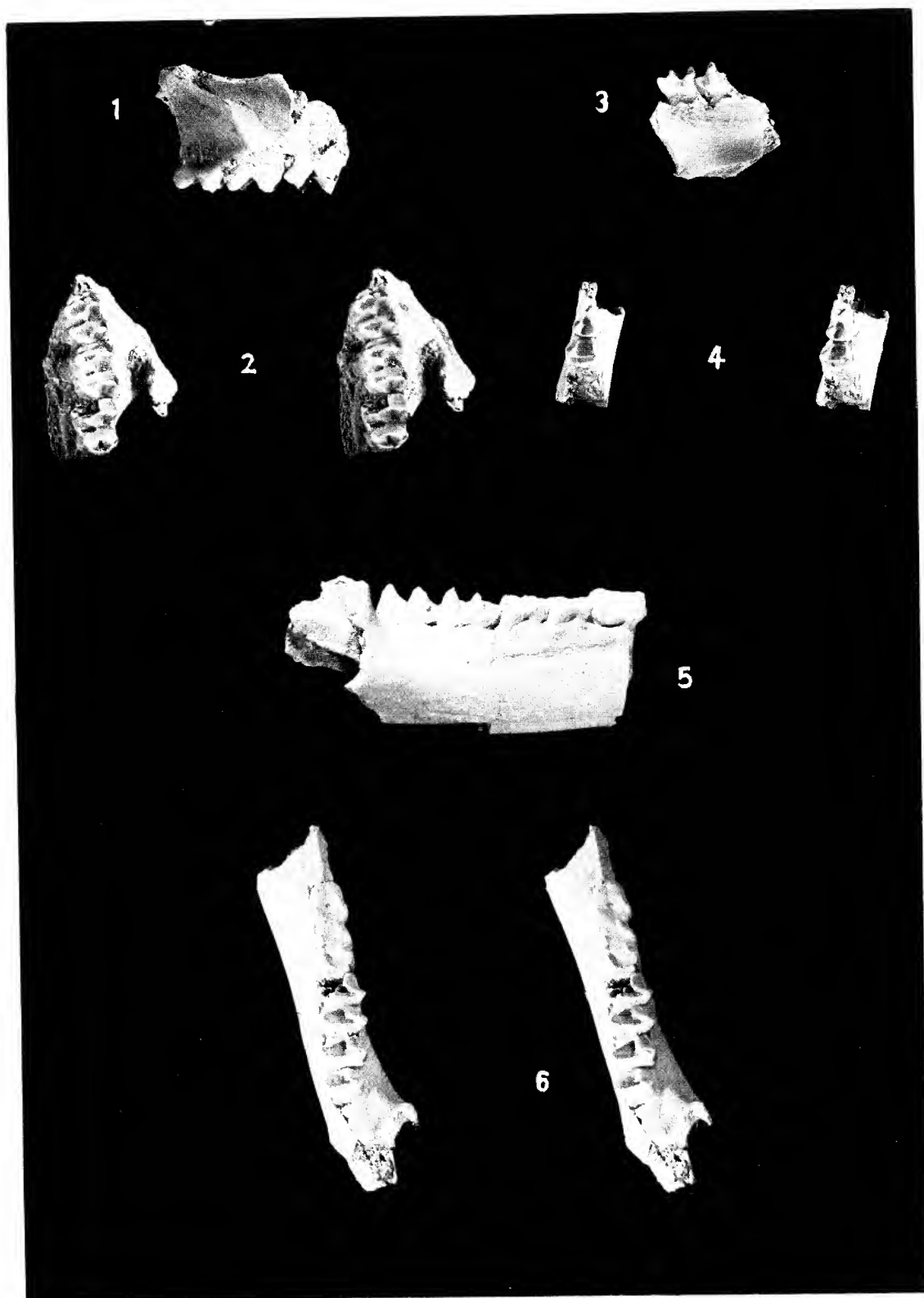
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PLATE 53

Wallabia indra (De Vis, 1895)

- FIG. 1: Lateral view of adult maxilla, F4740, Chinchilla Sand, Chinchilla, Darling Downs, $\times 1$.
FIG. 2: Stereopair of occlusal view of F4740, $\times 1$.
FIG. 3: Lateral view of juvenile mandible, F4749, western Darling Downs, $\times 1$.
FIG. 4: Stereopair of occlusal view of F4749, $\times 1$.
FIG. 5: Lateral view of adult mandible, F4741, Dalby, at 34–35 feet in pump well, Darling Downs, $\times 1$.
FIG. 6: Stereopair of occlusal view of F4741, $\times 1$.





RESULTS OF THE RAY E. LEMLEY EXPEDITIONS, PART 1. THE ALLINGHAM FORMATION AND A NEW PLIOCENE VERTEBRATE FAUNA FROM NORTHERN QUEENSLAND

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ABSTRACT

The Allingham Formation, a lake and stream deposit with a rich fauna of fossil vertebrates, contains some boulders of basalt. It is paraconformably overlain by part of the earliest known phase of the Nulla Basalt, the Allensleigh 'flow' which has given dates varying from 4.5 to 4 Myr. The fossiliferous deposit may result from damming by early flows and fit stratigraphically between the earliest and main flows of the Allensleigh Phase. The age is thus Lower Pliocene, and the fauna is significant for correlation as well as containing the first known occurrence of *Perameles allinghamensis* n. sp., *Phascolonus lemleyi* n. sp., and *Koobor jimbarratti* n. gen and sp. The fauna, referred to as the Bluff Downs local fauna, is similar to but apparently slightly older than the Chinchilla local fauna. This assessment is based on a consideration of the structurally more ancestral character of some of the Bluff Downs species. This supports the suggestion of Bartholomai (1972) that the Chinchilla local fauna is late Pliocene in age. Faunal differences from comparable Kalimnan faunas such as the Hamilton and Kanunka local faunas are attributed to slight age differences, different geographical or ecological settings, or different modes of accumulation.

Fossil bones were discovered, collected, and reported to the Queensland Museum in 1973 by Messrs J. Barratt and W. Snewin of Ayr. Following information from Mr Barratt that the outcrop underlay basalt, Museum collecting trips were made to the area in 1973 and 1974; both parties were ably assisted by Mr Barratt. Dr Ray E. Lemley participated in and helped to finance the second trip. Specimens described below are deposited in the Queensland Museum.

The geology is the joint responsibility of both authors. The taxonomic work has been carried out by Archer.

THE ALLINGHAM FORMATION

The name Allingham Formation is proposed here for the sequence of terrigenous clays, silts, sands, calcareous sands, and *Chara* limestones underlying the Allensleigh 'flow' of the Nulla Basalt, overlying laterite, and outcropping on Bluff Downs Stn, along the banks of Allingham Creek (at Lat. 19° 43'S, Long. 145° 36'E) a tributary of the Burdekin River, north Queensland. The type section (position indicated in Fig. 1A, B, and strati-

graphic columns detailed in Fig. 2) is the western end of the most extensive outcrop, on the north bank of Allingham Creek, 5.6 km west of Emu Valley Homestead. The name Allingham Formation is in reference to Allingham Creek. The thickness at the type section, which is also the most extensive vertical outcrop observed, is 18 metres.

As indicated in Fig. 2, lateritic detritus is present in whatever portion of the Allingham Formation overlies the laterite. At and adjacent to the type section this largely detrital bed has an independent character (Fig. 1B, a; Fig. 2, a). Here it is a fine ochraceous sediment with laterite clasts and light-coloured component which is now decalcified apart from one thin lens of *Chara* limestone (Fig. 2, section 2); its upper part is a claystone of titrated laterite which grades upward into a grey sandy silt, which is the base of a series of sands and silts (Fig. 1B, b; Fig. 2, b). These beds change upward again gradationally, into sandy *Chara* limestone (Fig. 1B, c; Fig. 2, c) with rare patches of secondary silicification, which in turn grades up into sands and clays (Fig. 1B, d; Fig. 2, d). In creeks at the north end of the amphitheatre (Fig. 1A), 0.2 km north of Allingham Creek, a brownish-grey clay is the

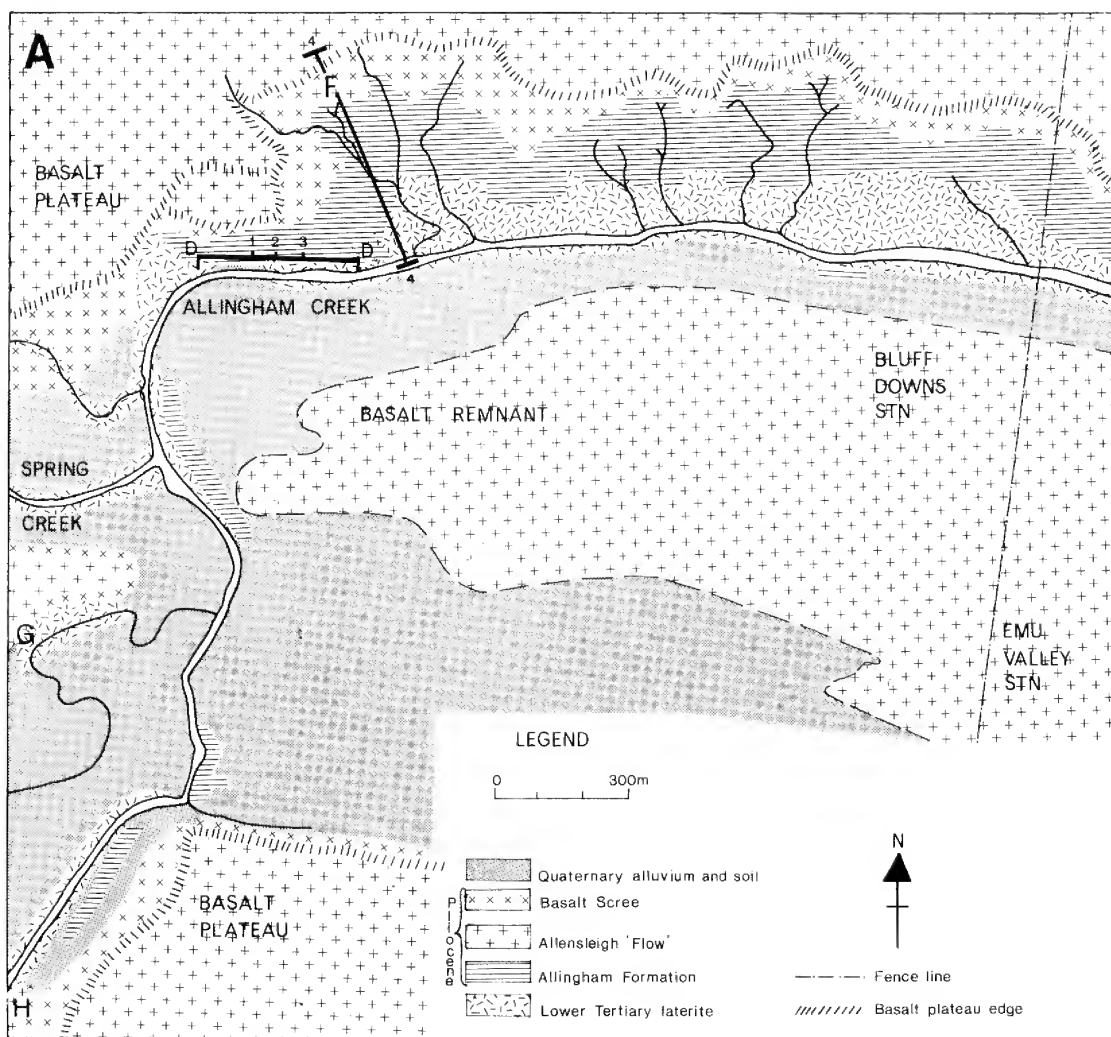


FIG. 1A: Locality plan of Allingham Creek showing type section (D-D) of Allingham Formation. F-H = exposed contacts of Allensleigh flow with: F, Allingham Formation; G, H, laterite mottled zone. Line D-D indicates position of largest cliff exposure of Allingham Formation with 1-3, positions of sections. Details of section stratigraphy shown in Fig. 2. Line 4-4 indicates non-vertical transect which is presented as vertical section 4-4 in Fig. 2.

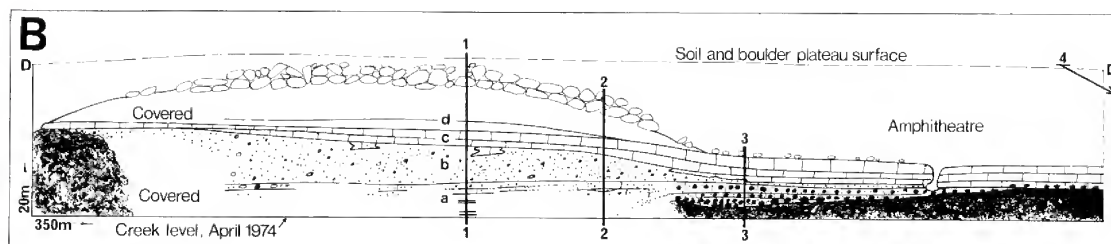


FIG. 1B: Face of cliff exposure (D-D of Fig. 1A) along Allingham Creek, type section. Positions of sections (1-3) are also shown. The laterite basement is deeply eroded and the sediments filling the hollows (bed a) contains much more laterite detritus than overlying beds (b-d). Stratigraphic positions of a-d are also indicated in Fig. 2.

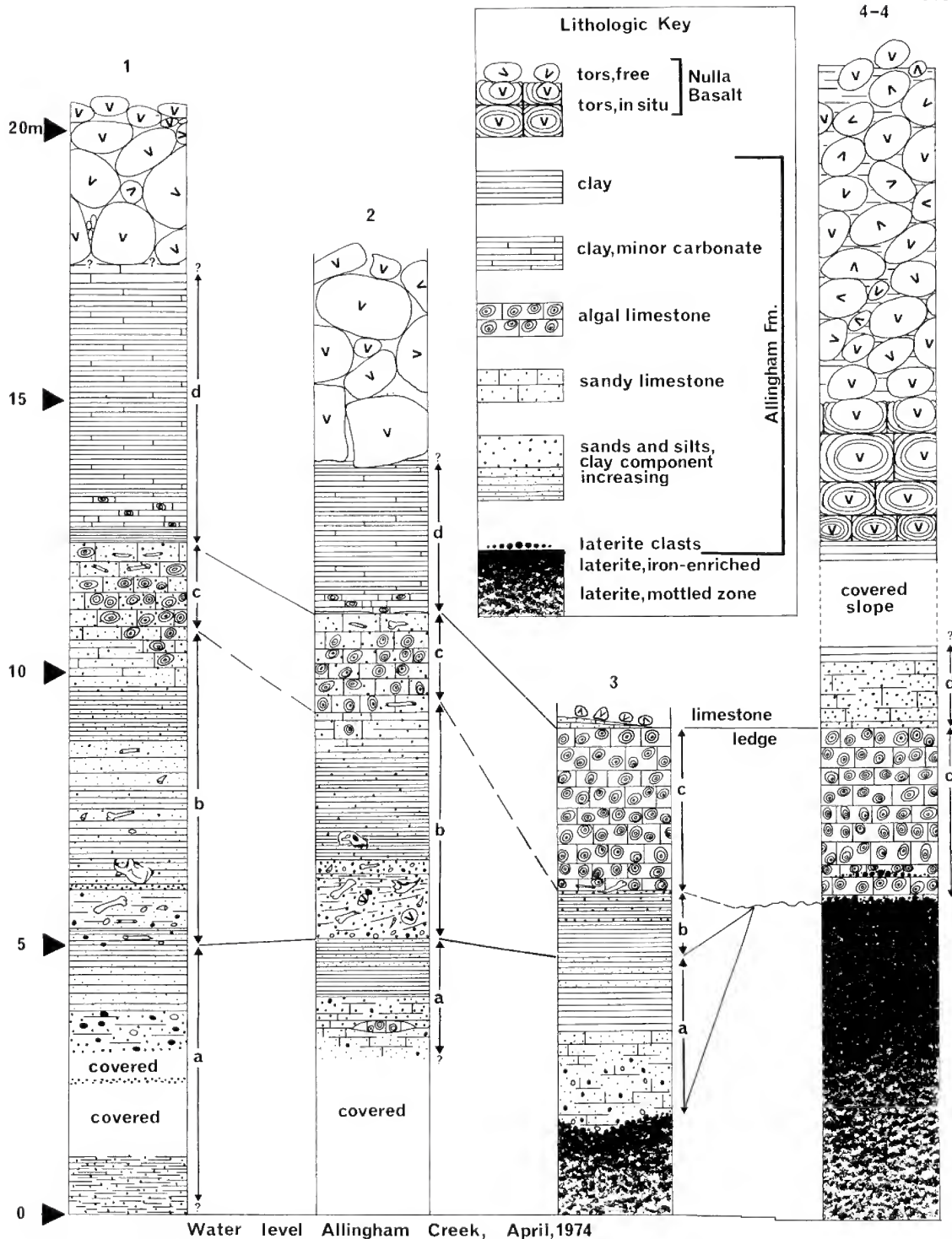


Fig. 2: Stratigraphic sections (1-3) of Allingham Formation along face of cliff exposure (D-D of Fig. 1A) or interpreted (4-4) from exposures along transect (4-4, Fig. 1A) north and east of cliff exposure. Vertical sections 1-3 and lower part of 4-4 were measured; the upper gently sloping part of section 4-4 was estimated. Beds a-d are informal designations of similar lithology. The top of bed d in section 1 and section 2 has not been observed because it is covered by basalt tors. The base of bed a is partly below the water level of Allingham Creek.

uppermost of the horizontal beds of the Allingham Formation. This is not likely to represent volcanic ash as it does not occur in the type section along Allingham Creek (Fig. 1B).

The general area has been described by Wyatt and Webb (1970) in the course of mapping and dating the flows of the Nulla Basalt (see also Wyatt 1968, 1969; Wyatt *et al.* 1965, geological map). The fossil occurrence on the eastern extremity of Bluff Downs station was straddled by traverses, and its area mapped by photo interpretation (Wyatt and Webb 1970, fig. 1) as covered by the Allensleigh 'flow'. Here Allingham Creek has cut through the basalt and the fossiliferous deposit into the widespread and deep laterite that Wyatt and Webb describe as basement in Basalt River just to the north. They correlate this laterite with the widespread and deep laterite that Exon, Langsford-Smith and McDougall (1970) date as older than basalts of 23 ± 1 million years, in an area running north from Amby to the level of Injune. In the area exposed by Allingham Creek there is a trend for the more westerly exposures of laterite to be stripped to mottled zone, while more easterly exposures have a varying thickness of iron-rich laterite crust preserved. Surface irregularity was several metres and at the northwesternmost exposure the fossiliferous beds wedge out between the laterite mottled zone and the basalt. To the north and east a ledge-forming *Chara* limestone forms most of the fossil beds and has been traced continuously for 3 km east of the main fossil localities. The top of the bed approximates the 1100' contour throughout its known extent (contours from Hillgrove 1:100,000 military map series R631, sheet 8058). It extends further than it was followed, and has been observed as an outlier on the road 1 km NE. of Emu Valley Homestead, another 4 km to the east, lying directly on laterite weathering to buckshot gravel. In this spot the Allensleigh 'flow' is reduced to loose boulders. This is probably the outcrop of limestone Wyatt (1969, p. 302) describes as '... on the track to Emu Valley Homestead ...' and likens to '... that which occurs as old lake or swamp deposits west of Eumara Springs Homestead ...' without giving distances or stratigraphic data. The latter locality is not specifically mentioned by Wyatt and Webb (1970) and must be relocated to find its relationship to the Allensleigh 'flow'.

In the Allingham Creek area on Bluff Downs, the Allensleigh 'flow' is usually seen as a jumble of small tors overlying the fossiliferous sediments or the lateritic basement. Original contacts have been noted in three places (Fig. 1A, F-H). In all three, deep tor weathering has occurred but, without the physical removal of weathered material from

between the tors, ground water still continues its attack. The continuous basalt is now much more deeply weathered than the free tors. In the absence of erosion surfaces or other divisions between them, this physico-chemical explanation for the differential weathering seems more likely than differing ages, especially as two of these occurrences occupy lows in the lateritic basement (south and west of the fossiliferous deposits) and one overlies the fossiliferous deposit. Wyatt (1969) reached a similar conclusion studying exposures to the north, notably in Basalt River. At the back of the shallow amphitheatre surrounding the outcrop shown in Fig. 1A, F; Fig. 2, 4-4, the strongly weathered basalt lies conformably on a brownish-grey clay overlying a metre of limey sand which in turn grades into 3 metres of hard *Chara* limestone. This limestone unconformably overlies iron-enriched laterite crust and has a basal conglomerate of buckshot gravel and finer laterite detritus. Traced westwards, along Allingham Creek, the limestone overlies laterite mottled zone and much of it changes laterally to sands and clays. Some of these are channel deposits which contain a minor amount of basalt as boulders and pebbles. These must indicate a basalt earlier than the Allensleigh 'flow' or the early extrusion of part of the 'flow'. Wyatt and Webb have already stated that the datings obtained on this 'flow' range from 4.5 Myr, 10 km WNW. near Bluff Downs Homestead, to 4 Myr further north (both datings $\pm 3\%$). They suggest the 'flow' may more properly be regarded as a flow series with a span of at least half a million years. The presence of basalt boulders in sediment underlying the main flow lends weight to their suggestion but does not rule out an earlier phase of the Nulla Basalt, possibly of minor extent. Neither interpretation is at variance with the visual evidence of conformity between the top of the fossiliferous sediment and the local base of the Allensleigh Phase. The fossiliferous sediment is thus dated as no less than 4 ± 1.2 Myr and not much older, i.e. Lower Pliocene (Harland, Gilbert Smith, and Wilcock 1964; Riedel 1973).

Observation of the lateral extent of the fossiliferous beds is hampered by the basalt cover and by Pleistocene channel deposits related to a roughly parallel course of Allingham Creek, which cut the deposit in two. The fossiliferous beds are probably an age-equivalent to the unconsolidated sands below the Allensleigh Phase at Eumara Springs (Wyatt and Webb 1970, pp. 40, 47). These are roughly 30 m lower than the fossiliferous beds, and 24 km to the east of the outlier on Emu Valley road. Both also could be age-equivalents of the Campaspe Beds, which are poorly dated, if the older of

the possible dates Wyatt and Webb suggest applies to the Campaspe Beds; even if this should be so, the deposits were not in lateral continuity and the strong limestone component provided by the growth of *Chara* gives the fossiliferous deposits described here a distinctive lithology over most of their outcrop.

Apart from the cliff containing the type section, outcrops of the terrigenous lower members of the Allingham Formation (a and b) are confined to the southern to eastern side of Allingham Creek and to its bed. The easternmost terrigenous outcrop yet found is 1 km west of the Emu Valley–Bluff Downs boundary fence and lies on lateritic mottled zone. It may have been covered directly by the basalt as its top is indurated, but erosion has removed an upper contact. A major outcrop, capped by *Chara* limestone, runs south from opposite the entry of Spring Creek, a western tributary, for about 300 m. This outcrop contains a very strongly calcareous development of bed c, *Chara* limestone in close-packed lenses. Here the limestone laterally replaces sand, both lateral equivalents overlying 0.5 m of derived laterite lying on laterite mottled zone *in situ*. The remaining southern outcrop is from 1 to 1.4 km south of the type section, and is fossiliferous sands and clays overlain by basalt. Outcrops in the creek bed are of a temporary nature due to shifting alluvium. They occupy pockets in the laterite.

The conditions of deposition indicated by the sediments show that the laterite surface was partly stripped and deeply gouged, before its flooding by water sufficiently permanent both to accumulate sediment and allow the growth of the widespread *Chara* flora. This flora, together with waterlaid sands, clays and channel deposits, suggests that an existent stream widened into a shallow lake. Animal fossils are relatively rare in the widespread limestone and are mainly scattered tortoise plates. In contrast, the terrigenous sediments contain many broken bones, some complete bones and skulls, and rarely articulated bones. By far the most common fossils throughout are scattered tortoise plates and crocodile teeth. Fish remains are relatively rare, which may indicate a seasonal constriction of the water body. Then, as now, the area sloped gently eastward (Wyatt and Webb 1970), and evidence of diastrophism, other than that provided by partial stripping of the laterite, is lacking. The cause of this erosion is scarcely likely to have been the damming mechanism which started deposition. The presence of a limited amount of basalt in some of the channel deposits suggests another mechanism, damming by a more easterly flow or portion of a flow, than supplied the basalt boulders.

BLUFF DOWNS LOCAL FAUNA

Michael Archer

The Bluff Downs local fauna is described below and may be summarized as follows. Dental terminology follows that used by Archer (1974, 1975a). Local fauna refers to a faunal assemblage from a particular area in the sense used by Tedford (1970); it is an informal term. Prefixes to specimen numbers include AM, Australian Museum; WAM, Western Australian Museum; J or JM, Queensland Museum modern specimens; F, Queensland Museum fossil specimens.

ARTHROPODA

Crustacea

Unidentified gastrolith

OSTEICHTHYS

Teleostei

Unidentified spines and vertebrae

REPTILIA

?Cheliidae

?*Chelodina* sp.

Crocodylidae

Palimmarchus sp.

Agamidae

Small unidentified agamid similar to *Amphibolurus* spp.

Varanidae

Varanus sp.

Boidae

?*Morelia* sp.

?Elapidae

Small vertebrae

AVES

Ciconiidae

Xenorhynchus asiaticus (Lathan, 1790)

MAMMALIA

Peramelidae

Perameles allinghamensis n. sp.

Vombatidae

Phascolonus lemleyi n. sp.

Phascolarctidae

Koobor jimbarratti n. gen. and sp.

Thylacoleonidae

Thylacoleo sp.

Macropodidae

Protemnodon sp.

Macropus sp. cf. *M. dryas* (De Vis, 1895)

M. (Osphranter) sp. cf. *M. woodsi* Bartholomai, 1975

Macropodid similar to *Thylogale*

Small macropodid, genus indet.

Diprotodontidae

Zygomaturus sp.

Euryzygoma sp.

Nototheriine, genus indet.

Unidentified families

One tooth fragment

Coprolites

SYSTEMATICS

ARTHROPODA

CRUSTACEA
(Plate 54f)

F7829 represents a crustacean gastrolith, the only specimen recovered.

OSTEICHTHYS

TELEOSTEI
(Plate 54a-b)

Fish spines (e.g. F7771) and vertebrae (e.g. F7772) are small and relatively uncommon. The largest vertebra is only 7 mm in diameter and the largest spine is 25 mm long.

REPTILIA

?CHELIIDAE

Fragments of tortoises were the most common fossils. These cannot at present be referred with any certainty to a particular species or even genus. A comparison of various Allingham fragments with materials described by De Vis (1894, 1897) as *Chelymys uberrima*, *C. arata* and *Chelodina insculpta* show some similarities. A fragment (F7796) possibly referable to *Chelodina* exhibits curious pock-markings, presumably the result of disease or invertebrate predation.

CROCODYLIDAE

Crocodylian teeth are the next most common vertebrate remains. Variation in form and size is considerable and it is possible that more than one species is represented. As well as teeth there are large crocodylian vertebrae, limb bones, scutes and skull fragments.

Palimnarchus sp.
(Plate 54 c-e)

Large compressed teeth (e.g. F7763, Plate 54d) with serrated edges probably represent a species of this genus. Almost identical teeth occur in the Chinchilla Sand. Some Allingham teeth (e.g. F7764, Plate 54e), show occlusal wear, a not uncommon characteristic of *Palimnarchus* (M. Hecht, pers. comm.).

Several small crocodile teeth (e.g. F7767, Plate 54c) exhibit extensive vertical fluting. In *Crocodylus johnstoni*, this feature is common in most teeth. In *C. porosus* it sometimes occurs on smaller but not larger teeth. It may similarly have occurred on some teeth of *Palimnarchus*, and cannot be used to

distinguish a second taxon unless associated material proves distinctive. Longman (1924) describes *C. nathani* from fossil material found at Tara Creek, Maryvale Station, north Queensland. This species is dubiously distinct from *Palimnarchus* and no attempt has been made to distinguish it among the Allingham crocodylian remains.

A thorough revision of late Cainozoic crocodylians must be made before all the Allingham crocodile remains can be positively identified.

AGAMIDAE
(Plate 54i)

A small right dentary fragment (F7812) with seven teeth represents an agamid lizard similar to some species of *Amphibolurus*.

VARANIDAE

Varanus sp.
(Plate 54h, j)

At least two vertebrae (F7774, and F7777) represent a species of this lizard genus. A recurved tooth crown (F7813, Plate 54h) may also be referable to *Varanus*. The tooth is 15 mm long and 6 mm wide at the base, somewhat polished by stream-abrasion, without serrations on posterior or anterior cutting edges, and lacks vertical fluting around the crown base.

In modern comparative material of *Varanus* the teeth have very fine serrations on anterior and posterior cutting edges as well as vertically fluted crown bases. In *Megalanias prisca*, *Varanus dirus* and *Notiosaurus dentatus* these same characters occur, except that the anterior cutting edge has fewer serrations than the posterior edge.

Fejérvary (1918) refers *Notiosaurus* to *Megalanias* and suggests that material previously referred to *V. dirus* may represent two forms: the holotype, which comes from the Darling Downs, possibly representing *Megalanias prisca*; the referred specimen, which comes from Chinchilla, representing something else. *Varanus emeritus* is not represented by teeth. Of all these fossil varanids and megalanids the Allingham tooth is most similar to the referred specimen of *V. dirus* from Chinchilla but differs in being less recurved and in lacking the serrations and vertical fluting. Its degree of recurving is matched by some modern *Varanus* (e.g. *V. varius*) and it is possible that if fluting and serrations were fine enough on the Allingham tooth, they could have been removed by abrasion.

The single Allingham tooth is twice the size of teeth of a seven foot specimen of *Varanus salvadorii*, the largest specimen of a species of *Varanus* in

the Queensland Museum. The fossil tooth differs morphologically in having a wider and less slender crown, and a more rounded anterior cutting edge.

One of the Allingham varanid vertebrae (F7774, Plate 54j), a posterior rib-bearing lumbar vertebra (around the 21st or 22nd position), is similarly unique. It compares favourably with vertebrae of *Varanus* species but not *M. prisca*. Vertebrae of megalanids from Chinchilla have not been described. The Allingham vertebra differs from comparably sized vertebrae of *V. salvadorii* in being markedly taller, having an antero-posteriorly shorter neural spine, a pronounced vertical crest on the posterior edge of the neural arch, and sub-rounded, more vertically inclined prezygapophyses.

The other varanid vertebra (F7777), an anterior caudal vertebra of uncertain position, is about equally distinct from modern species of *Varanus*. The ventral pedicels for the haemal arch, the relatively anteriorly situated cotyle, and the relatively reduced neural spine indicate that this vertebra represents a varanid, but the pronounced ventral crest, relatively high neural arch and reduced transverse processes are unmatched by vertebrae of any modern species with which comparison has been made (*V. salvadorii*, *V. varius* and *V. gouldii*).

BOIDAE (Plate 54k)

Three vertebrae (including F7775) represent a very large boid, morphologically very similar to modern species of *Morelia*. No comparative material has been available in the size range of this Allingham snake, so minor differences in morphology may be attributed to allometry.

It is difficult and often misleading to estimate sizes of animals based on fragmentary remains, but compared with a 5.3 m specimen of *Morelia spilotes*, the Allingham boid may have been over 6.2 m long. Worrell (1970) notes a record of a modern Australian boid (*Liasis amethystinus*) of 8.7 m. Considering this, the Allingham snake was probably no larger than some modern boids.

?ELAPIDAE (Plate 54g)

Two small vertebrae (including F7826) may represent elapids. They compare favourably with species of *Pseudechis* but not enough colubrid material has been available to be certain of even the familial identity of these vertebrae.

AVES CICONIIDAE

Xenorhynchus asiaticus (Lathan, 1790)

A fragment of a tarsometatarsus (F7036) represents this modern stork (pers. comm. J. van Tets, 21.i.1974) known as the Blackheaded Stork.

Other bird remains are presently under study by P. Rich.

MAMMALIA PERAMELIDAE

Perameles allinghamensis n. sp. (Fig. 3; Plate 55c)

HOLOTYPE: F7821, isolated RM²; Allingham Formation, Lower Pliocene, site 5, Allingham Creek, Bluff Downs Stn, north Queensland.

DIAGNOSIS: Very large peramelid differing from other species of *Perameles* in having better-developed antero-buccal cingulum; more closely approximated protocone and paracone; paracrista which buccally contacts stB which is posterior to parastylar corner of tooth.

DESCRIPTION: Measurements shown in Fig. 3.

Crown showing slight wear on tips of all cusps. Metacone broken and metastylar corner missing. Tip of hypocone damaged. Anterior cingulum short and complete but just barely so beneath paracrista. Anterior cingulum formed by confluence of antero-buccal cingulum and preprotocrista. Postprotocrista descends to meet on hypocone (or metaconule). Crest leaves hypocone postero-buccally and descends to base of metacone where it forms very short, reduced posterior

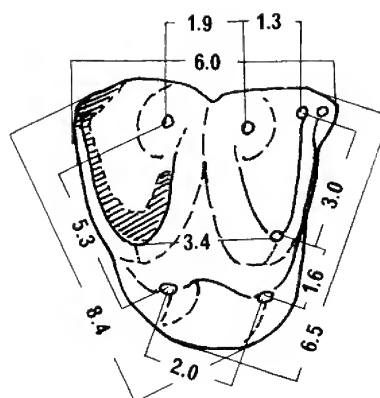


FIG. 3: Measurements (mm) of F7821, RM², holotype of *Perameles allinghamensis* n. sp. Hatched area indicates damage.

cingulum before terminating along flank of metacone. Hypocone small and separated from protocone by deep vertical fissure on postero-lingual face of crown. Metacone higher than subequal paracone and protocone which are higher than hypocone. StB shorter than large subequal stC and D. StA indistinguishable from parastylar corner of tooth but short buccal crest links stB with antero-buccal cingulum. This crest may be homologue of stA. Anterior paracrista (homologue of dasyurid paracrista) forms prominent crest linking paracone and stB. Posterior paracrista similarly links paracone and stC. Prominent anterior metacrista links metacone and stD. Posterior metacrista (homologue of dasyurid metacrista) damaged but presumably extended to metastylar corner of tooth. Presence or absence of stE unknown. Prefossa between bases of protocone, paracone and metacone extends to buccal surface of crown. No crest links stC with D. Similarly, no crest links stB with C. StC gently recurved anteriorly. StD gently recurved posteriorly. Ectoloph virtually non-existent as result of failure of stylar cusps to be united by crests. Ectoflexus greatest between stC and D.

This tooth is considered to be an M^2 because of the size of the stylar cusps, hypocone and relative sizes of the paracone and metacone.

DISCUSSION: Species of *Perameles* available for examination have been *P. nasuta* (e.g. J10816), *P. bougainvillei* (e.g. WAM M10576), *P. eremiana* (WAM M1575), and *P. gunnii* (e.g. AM M2640). This includes all modern species recognized by Ride (1970). Most species of the genera *Microperoryctes*, *Peroryctes*, *Echymipera*, *Isodon*, *Chaeropus*, *Macrotis* and *Ischnodon* have been examined. Photographs of the only known material of *Rhynchomeles* have been made available by courtesy of the British Museum. This includes all modern and fossil perameloid genera recognized by Tate (1948) and Stirton (1955).

P. allinghamensis occupies a somewhat intermediate structural position between *Perameles* and those species of *Echymipera* which have been examined (*E. rufescens*, both subspecies, and *E. kalubu*). As in other species of *Perameles*, stC of *P. allinghamensis* is relatively discrete and conical on M^2 . This is true but to a lesser extent in species of *Echymipera* where stC is sometimes linked to the paracone by a small crest. This latter condition is common and better-developed in other peramelids such as *Peroryctes* and *Microperoryctes*. The anterior cingulum is better-developed in *Echymipera* than it is in *Perameles* and in this respect *P. allinghamensis* resembles *Echymipera*. *P. alling-*

hamensis may be an ancestor of *Perameles*, *Echymipera*, or both. It is referred here to *Perameles* because of the crest and stylar cusp morphology. When more material is discovered, it is probable that it will warrant generic separation from all modern peramelids.

Other fossil perameloids include *Ischnodon australis* (referred elsewhere to the Thylacomyidae, Archer and Kirsch in preparation); an unnamed peramelid from the Hamilton local fauna (Turnbull and Lundelius 1970) represented by fragments of lower molars; *Perameles tenuirostris* Owen which is regarded by Lydekker (1887) as synonymous with *P. nasuta*; *P. wombeyensis* which has been synonymized with *Isodon macrourus* by Wakefield (1972); and an unnamed peramelid from the Fisherman's Cliff local fauna (Marshall 1973) represented by a fragmentary upper molar. There is some doubt about the provenance of this last specimen (Mr P. Crabb, pers. comm.). The possible peramelid noted by Woodburne (1967) from the Miocene Alcoota local fauna now appears to represent a thylacoleonid (Dr W. A. Clemens, pers. comm.).

ORIGIN OF SPECIFIC NAME: The specific name is in reference to the Allingham Formation and Allingham Creek.

VOMBATIDAE

Phascolonus lemley n. sp.

(Fig. 4; Plate 56)

HOLOTYPE: F7819, left dentary with M_{1-4} ; Allingham Formation, lower Pliocene, site 5, Allingham Creek, Bluff Downs Stn, north Queensland.

REFERRED MATERIAL: F7818, LI_1 ; F7768–70, isolated molars: same locality as holotype.

DIAGNOSIS: Very large vombatid, differing from *Phascolonus gigas* in markedly longer dorso-ventral section of I_1 ; shorter cheek-tooth row; shallower masseteric fossa; smaller and less protruding ventro-lateral rim of masseteric fossa; broader posterior border of dentary below articular condyle; shallower symphysis; and edge of ectocrotaphyte plate and articular condyle which extend relatively farther postero-dorsally. Differs from *Phascolomys magnus* and *P. medius* in being larger; having markedly longer dorso-ventral section of I_1 ; proportionately much longer premolar; and deeper masseteric fossa. Differs from all other vombatids in its much larger size as well as morphological characters.

DESCRIPTION: Measurements shown in Fig. 4.

Dentary broken at point anterior to mental foramen and posterior to I_1 alveolus. Coronoid

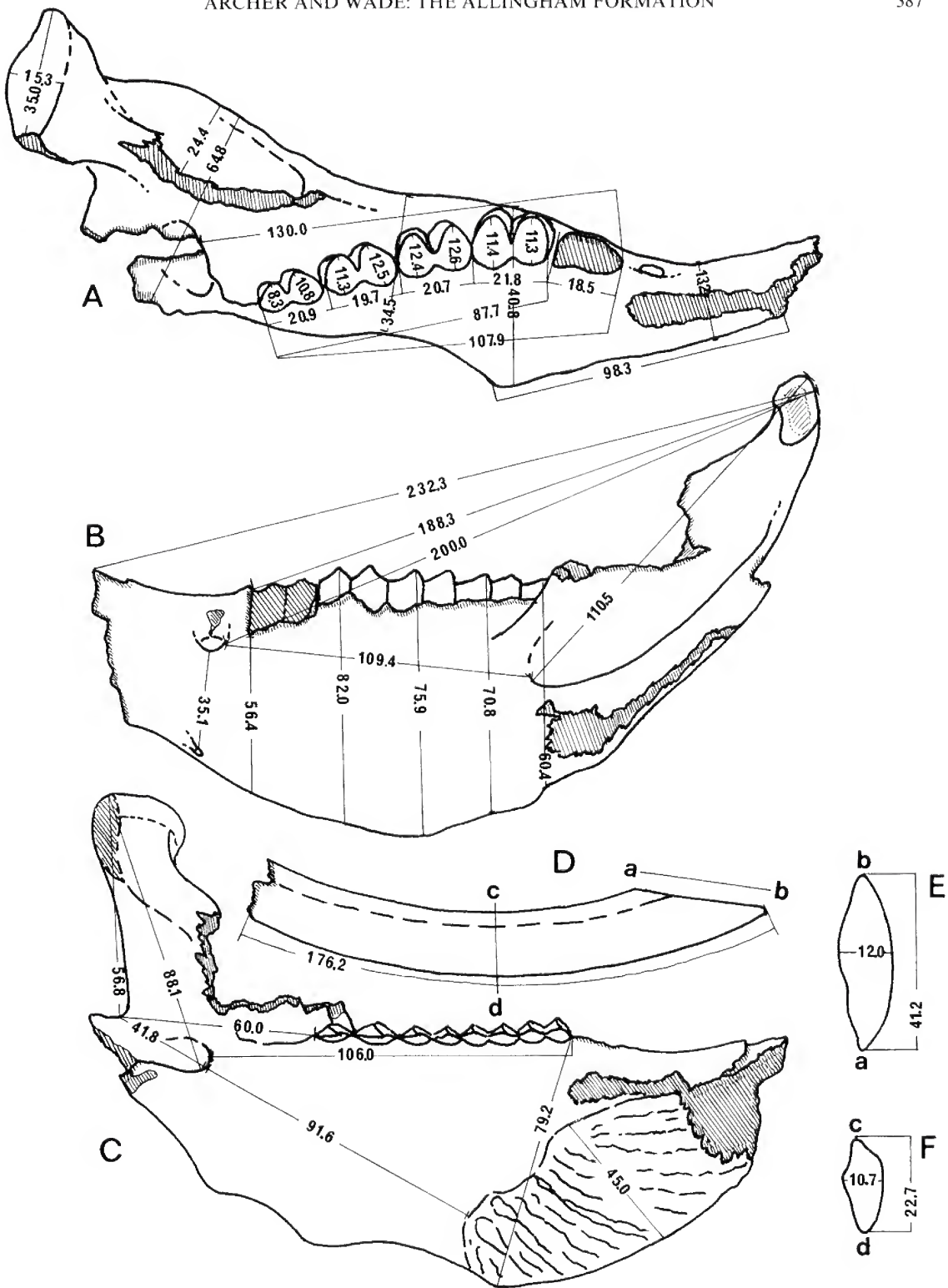


FIG. 4: Measurements (mm) of F7819, holotype of *Phascolonus lemleyi* n. sp., and F7818. A-C, F7819, left dentary with M₁₋₄. D, F7818, LI₁. Hatched areas indicate damage.

and angular processes broken at bases. Mesial and distal tips of articular condyle broken. I_1 and P_4 missing, although proximity of LI_1 (F7818) to dentary in quarry (less than 20 cm), unabraded condition of open root of I_1 and alveolus of I_1 indicate that isolated I_1 probably drifted out of dentary shortly before burial. Associated with dentary in same quarry 10 cm away was an articulated macropodid hindlimb, suggesting that adjacent objects in quarry may be parts of one individual.

I_1 with flat horizontal occlusal surface. Wear striae on occlusal surface extend antero-posteriorly from anterior tip for distance of 39 cm, presumably distance through which dentary dislocates during thegnosis. Prominent ventral keel. Dorsal surface forms narrow shelf which inclines lingually. Prominent depression runs length of I_1 on dorsal-buccal surface. Less pronounced longitudinal striae run length of I_1 .

P_4 alveolus indicates tooth had only very shallow medial lingual groove, although there were two poorly differentiated (in comparison with molars) columns. Alveolus length suggests P_4 slightly shorter than M_1 .

M_{1-4} markedly divided into two columns, buccal grooves being sharper and more deeply incised than lingual grooves. Talonid (posterior column) wider than trigonid (anterior column) in M_1 , subequal in M_{2-3} and narrower than trigonid in M_4 . Worn trigonid height subequal to worn talonid height M_{1-2} , but taller than worn talonid M_{3-4} . Talonid length longer than trigonid length M_1 but shorter than trigonid length M_{2-4} .

Dentary massive (but markedly less so than in *P. gigas*). Symphysis extends posteriorly to level of middle of M_2 . Base of ascending ramus leaves body of dentary at level of anterior end M_4 . Masseteric fossa deep for a vombatid but shallow compared with *P. gigas*. Postalveolar ridge sharply curved postero-laterally and forms dorsal rim of dental canal. Pre-alveolar ridge forms sharp crest which extends as far anteriorly as broken anterior edge of dentary. Ectocrotaphyte plate relatively narrow (compared with *P. gigas*). Mylo-hyoid groove relatively large. Width of superangular cavity (pterygoid fossa) exceeds that of ectocrotaphyte plate. Inferior dental canal has large orifice (mandibular foramen) but rapidly tapers down to small canal. Masseteric foramen very large, almost as large as mandibular foramen.

Ectocrotaphyte ridge and articular condyle extend postero-dorsally farther than they do in material described by Stirling (1913). Posterior neck of dentary below condyle broad and flat,

unlike condition illustrated by Owen (1872, plate 138, fig. 1) but somewhat similar to specimen described as 'Mandible "C"' by Stirling (1913). Compared with Owen's (1872, plate 36, fig. 1) illustration of *P. gigas*, ascending ramus of *P. lemleyi* exhibits longer masseteric fossa, and longer and less-curved border anterior to articular condyle.

DISCUSSION: Wombats of the genus *Phascolonus* (*P. gigas* and *Sceparnodon ramsayi*) have all been placed in the synonymy of *P. gigas* Owen. The taxonomic positions of *medius* Owen and *magnus* Owen are unclear (Tate 1951). In some respects such as size and premolar morphology, they resemble *P. gigas* and make generic boundaries of *Phascolonus* difficult to recognize. Synonymy of *ramsayi* with *P. gigas* enables the generic diagnosis of *Phascolonus* to include widely spatulate upper incisors. Upper incisors of *P. lemleyi* are not yet known, but overall similarity of lower incisors of *P. lemleyi* to those of *P. gigas* suggest the upper incisors are spatulate. Differences in lower incisors of *P. lemleyi* and *P. gigas* include much longer cross-sectional length of the former which results in a relatively longer occlusal wear surface. Possible significance of this is not clear although increase in cross-sectional length of I_1 in other wombats appears to correlate with increase in width of I_1 such as may be observed in a structural sequence from *Vombatus ursinus*, through *Phascolomys magnus*, to *Phascolonus gigas*. If this relationship is maintained in *P. lemleyi*, its upper incisors were not only relatively but absolutely wider than those of *P. gigas*.

A specimen (F834) collected at Freestone Creek, Darling Downs, Queensland, resembles *P. lemleyi* in cross-sectional length of I_1 , and length of M_{1-4} . It differs in having a shorter P_4 comparable in size with *magnus*, and raises a question about the number of Pleistocene species of *Phascolonus*. Stephenson (1963) describes *Diarcodon parvus* as a diprotodontid similar to but smaller than *Sceparnodon ramsayi*, which he also regarded as a diprotodontid. There can be no doubt that *Sceparnodon* is a vombatid (Ride 1967) and the diprotodontid affinity of all of the material referred to *D. parvus* is doubtful. Some of the upper incisors may represent a species of *Phascolonus*.

ORIGIN OF SPECIFIC NAME: The specific name is in honour of Dr Ray E. Lemley, Queensland Museum Associate, who very kindly helped us on several occasions by financing and accompanying expeditions.

PHASCOLARCTIDAE

Koobor n. gen.

TYPE SPECIES: *Koobor notabilis* (De Vis) [= *Pseudocheirus notabilis* De Vis 1889].

DIAGNOSIS: Small phascolarctids, similar to *Phascolarctos* but differ in being smaller; lacking extensive fine crenulations on molar crown surface; lacking well-developed pockets or basins between bases of protocone and hypocone; having distinctly shorter and bicuspid P^4 without significant longitudinal crest development; having well-developed basin buccal to paracone between ectoloph, preparamacrista and postparamacrista; having stylar crests well-developed adjacent to stB; having well-developed gap between stC and stD; and overall crown outline which is relatively longer than wide. Differs from *Litokoala* in having narrower molars; better-developed and enclosed basin buccal to paracone; less crenulations; and no well-developed metaconule. Differs from *Perikoala* (as judged by comparison with fragmentary material described by Stirton, Tedford and Woodburne 1967) by having narrower and less crenulated molars. Differs from *Pseudokoala* and all pseudocheirines (*Pseudocheirus*, *Pseudochirops*, *Schoinobates*, *Pteropseudes*, *Hemibelideus*) in having lingually displaced paracone and metacone; lacking complex or well-developed metaconule on M^{1-2} ; lacking well-developed protoconule on M^{2-3} ; having better-developed anterior cusp on P^4 ; and having larger gap between stC and stD.

ORIGIN OF GENERIC NAME: Koobor is an Aboriginal mythological Koala-boy who was always so thirsty that he stole his companions water containers and hid with them up a tree. When discovered, he was punished by his enraged companions and turned into the Koala, a creature who thereafter never drank water (Roberts and Mountford 1970).

Koobor jimbarratti n. sp.
(Fig. 5; Plate 55b)

HOLOTYPE: F7822, isolated $RM^{1 \text{ or } 2}$, Allingham Formation, Lower Pliocene, site 5, Allingham Creek, Bluff Downs Stn, north Queensland.

DIAGNOSIS: Differs from *Koobor notabilis* (only other species) in having well-developed parastyle; poorly-developed anterior cingulum; preprotocrista which contacts preparacrista; more obtuse angle enclosed by pre- and postmetacristae; and poorly-developed buccal crests at ends of pre- and postmetacristae.

DESCRIPTION: Measurements shown in Fig. 5.

Transverse fracture occurs through tooth. Surface of enamel lightly pitted by chemical erosion. All primary cusps subequal in height. Metacone and hypocone just closer together than paracone and protocone. Preprotocrista contacts base of preparacrista midway along length of preparacrista. Postprotocrista passes postero-buccally to midline of tooth then joins prehypocrista. Posthypocrista passes postero-buccally to form small posterior cingulum before contacting buccal end of postmetacrista. Preparacrista short, markedly curved, and contacts stB. Postparacrista longer, less curved, and contacts stC. Pre- and postparacrista indirectly connected buccally by ectoloph crest connecting stB and stC. Premetacrista straight and runs to position of stD. Postmetacrista straight and runs to metastylar corner of tooth where it connects with upturned posterior cingulum. Low crest on ectoloph from buccal end of premetacrista does not extend posteriorly as far as metastylar corner. No crest connects stC and position of stD. Parastylar crest connects anterior end of preparacrista to parastylar corner of tooth. Below point of contact between preprotocrista and preparacrista, two small vertical crests connect short antero-buccal cingulum to premetacrista and preprotocrista, enclosing very small pocket between them. Antero-buccal cingulum poorly-defined or absent along lingual half of tooth, although basal crown swelling occurs. Shallow basin occurs between bases of protocone and hypocone. Side of tooth between pre- and postmetacristae not enclosed buccally. A lingual crest occurs on metacone extending antero-lingually to midcrown basin.

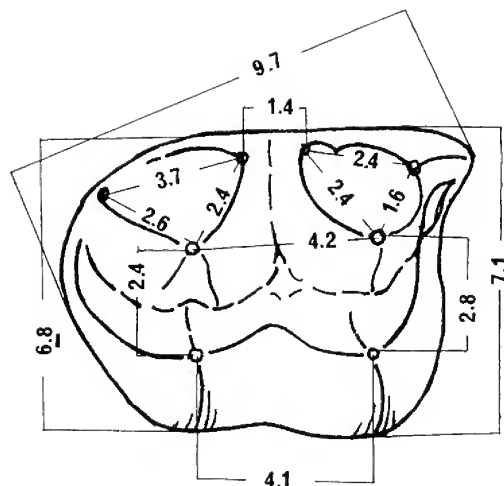


FIG. 5: Measurements (mm) of F7822, RM^1 or RM^2 , holotype of *Koobor jimbarratti* n. gen. and sp.

Smaller lingual crest extends postero-lingually from metacone tip to posterior cingular basin. Poorly-developed protocone rib extends buccally from protocone tip to base of metacone. Rib and crest development on paracone and protocone not clear.

DISCUSSION: The species of *Koobor* are clearly not pseudocheirines but they are similar to phascolarctids, and of these, perhaps closest to the middle Miocene *Perikoala*. They may be late Tertiary representatives of the same phascolarctid group. *Litokoala* and *Phascolarctos* are not representatives of this group and may have been independently derived from other Miocene phascolarctids.

The Chinchilla species is better known than the Allingham species and, in some respects such as the better-developed buccal basins, is structurally more advanced.

ORIGIN OF SPECIFIC NAME: *Koobor jimbarratti* is named in honour of Mr Jim Barratt who, with Mr Wally Snewin, originally discovered the fossil sites along Allingham Creek.

THYLACOLEONIDAE

Thylacoleo sp. (Plate 55a)

MATERIAL: F7762, right dentary fragment with half of P_4 and M_1 , roots of I_1 , and alveoli for M_1 ; F7807, posterior fragment of LP_4 ; F7808, posterior fragment of LP^4 .

DISCUSSION: This is a very small species of *Thylacoleo* comparable in size to a form recorded by Merrilees (1968, p. 14) as '*Thylacoleo*, probably not *carnifex*' from a paraconglomerate interpreted by Merrilees to be Pleistocene in age, at Wonberna, near Balladonia, Western Australia. It differs from this form in having a relatively much larger M_1 . It is also similar to *T. crassidentatus* from the Pliocene Chinchilla Sand, but differs in having a proportionately much shorter P_4 .

Thylacoleonids are separable into at least two distinct types: *Thylacoleo* species, so far known only from Pliocene and younger sediments; and *Wakeleo* species, so far known only from middle to late Miocene sediments. A third type may be represented by an undescribed form from the middle Miocene Etadunna formation. The Allingham form, although clearly referable to *Thylacoleo*, is also similar to *Wakeleo* in so far as it exhibits a relatively short P_4 and large M_1 . It is tempting to assume orthogenesis and see the Allingham thylacoleonid as a link in a chain

leading directly from *Wakeleo* to *Thylacoleo*. However this type of reasoning is almost always found to be fallacious when the fossil history of a group becomes better known. Indeed, the occurrence of a thylacoleonid with a short P_4 in supposedly Pleistocene deposits at Wonberna is sufficient reason to doubt that premolar length can be directly correlated with time. As in most groups, the late Tertiary radiation of thylacoleonids probably resulted in a complex of forms, each the product of different selective pressures, rather than all being subject to one single pressure, namely an increase in carnassial length at the expense of other cheek-teeth.

MACROPODIDAE

Comments about the forms represented here are only preliminary. Formal descriptions will be given by Archer and Bartholomai (in preparation). There are at least five macropodid species represented, of which four can be assigned to genera: *Protemnodon* sp.; *Macropus* cf. *M. dryas*; *Macropus* (*Osphranter*) sp.; and ?*Thylogale* sp. Concepts of Chinchilla species of *Macropus* employed here are those of Bartholomai (1975).

Protemnodon sp. (Plate 57a-b)

A maxilla (F7810), fragmentary upper premolar (F7814), isolated molars (e.g. F7809), and a dentary with dP_3 and M_1 (F7812) represent a small species of this genus. It is most similar in morphology to *P. chinchillaensis* and *P. devisi* from the Pliocene Chinchilla Sand and *P. otibandus* from the Pliocene Otibanda Formation. The upper molars of the maxillary fragment (F7810) differ from those of *P. devisi* in being smaller; lacking a lingual cingulum between the bases of the protocone and hypocone; having a less well-developed midlink, and a better-developed posterior pocket. They differ from *P. chinchillaensis* in having a wider metaloph on M^4 and a less well-developed midlink. Overall, they most closely resemble *P. chinchillaensis*. An isolated RM^4 (F7811) is even more similar to those of *P. chinchillaensis* than is the M^4 of F7810. It has a comparably developed midlink and a very narrow metaloph. The isolated RP^4 fragment (F7814) is relatively narrow and shows other differences that appear to distinguish it from *P. chinchillaensis*. Considering variation in premolar morphology shown by Bartholomai (1973), these differences may not be significant. DP_3 (F7812) however, appears to be markedly different from that tooth in *P. chinchillaensis* as well as *P. devisi*. The protoconid is either absent or in-

distinguishable from the metaconid, and the buccal side of the trigonid is incised by a prominent vertical fissure. There is also a buccal cingulum between the bases of the trigonid and talonid. It is possible that this single tooth is abnormal. Comparably unique though different morphologies are reported as abnormalities by Archer (1975b).

Detailed comparisons with *P. otibandus* will have to await formal description of the Bluff Downs material. Plane (1972) and Bartholomai (1973) indicate broad similarities between *P. otibandus*, *P. devisi* and *P. chinchillaensis*, and the apparently long geological history of at least *P. otibandus*, from late Miocene to late Pliocene time.

Macropus sp. cf. M. dryas (De Vis, 1895)
(Plate 57c-d)

This macropodid is well-represented by fragmentary dentaries (e.g. F7823), and maxillary fragments (e.g. F7780). F7823 closely resembles F2508 from Chinchilla which is referable to *M. dryas*. Differences include a slightly more massive P_3 which also lacks the prominent crest extending postero-lingually from the posterior end of the longitudinal crest; less antero-posteriorly oriented paracristid; narrower anterior cingulum on dP_4 ; and longer P_4 with fewer and less well-defined vertical ribs along the longitudinal crest. These differences appear reasonably constant in all specimens examined. Upper teeth also resemble *M. dryas*, and no consistent differences have been noted in premolar or molar morphology.

Macropus (Osphranter) sp., cf. M. woodsi Bartholomai, 1975
(Plate 57e)

F7785, an isolated RM^* represents a species of *Macropus* morphologically similar to *Macropus (Osphranter) pan* and *woodsi* from the Chinchilla Sand. It is approximately the size of *M. woodsi* and smaller than *M. pan*. Characters that suggest relationship with these Chinchilla species include a prominent isolated enamel crest or cusp buccal to the midlink in the buccal side of the mid-valley; relatively narrow anterior cingulum with forelink; midlink without accessory crests; and well-developed posterior pocket. This Allingham form, at present known from one tooth, could well prove to be an ancestor of either *Macropus woodsi*, *M. pan* or both.

Three isolated premolars (F7789-91) resemble those of modern *M. (Osphranter)* but may represent either *M. (Osphranter)* cf. *M. woodsi*, or yet another unknown, even unrelated, macropodid. An unworn LP^4 (F7791) shows a basic pattern

shared by many macropodine genera such as *Macropus*, *Petrogale*, *Prionotemmus*, and *Wallabia*, with a principal longitudinal ribbed crest supported at each end by a large cusp; well-developed lingual cingulum and cingular basin; low postero-lingual cusp connected to the longitudinal crest by a small transverse crest; and small posterior pocket formed between the transverse crest, the postero-lingual cusp, the large posterior cusp of the longitudinal crest, and a small posterior cingulum. A slightly worn LP_4 is more similar to that tooth in *Osphranter* than other forms examined. It is a simple tooth, indistinctly bilobed with a very reduced postero-lingual crest.

Cf. Thylogale

Two isolated lower molars (F7794-5) are difficult to distinguish from teeth of modern *Thylogale* but show too few distinctive structures to enable reference to any particular modern or fossil genus.

An isolated upper right molariform tooth (F7785) may represent a dP^4 and is similarly difficult to distinguish from corresponding teeth of *Thylogale* (e.g. *T. stigmatica*).

SMALL MACROPODINE
(Plate 57f)

F7784, an isolated lower molar, is unlike other Allingham macropodids noted above in possessing a relatively horizontal posterior cingulum, such as occurs in some *Protemnodon*. This feature combined with its *Macropus*-like crown morphology and small size makes it unlike any Pliocene or Quaternary macropodids examined.

DIPROTODONTIDAE

Zygomaturus sp.
(Plate 58d)

An isolated RP^4 (F7776) represents a species of *Zygomaturus*. Three species of *Zygomaturus* are currently recognized: *Z. trilobus* (many Pleistocene deposits); *Z. gilli* (Beaumaris); and *Z. keanei* (Alcoota). The Allingham *Zygomaturus* differs from all of these in having a much larger hypocone and smaller protocone so that transverse tooth width is markedly greatest along a line through the hypocone and metacone, and a much better developed buccal cingulum and cingular pocket.

Closer comparison may be made with an as yet undescribed specimen (F3829) of *Zygomaturus* from the Chinchilla Sand. The Chinchilla specimen is similar in having a large hypocone and a well-developed buccal cingulum. It differs from the

Allingham tooth in being much larger in all dimensions; in having an even longer buccal cingulum; and in having the protocone and lypocone farther apart. Other differences are obscured by wear on the Allingham specimen.

This zygomaticurine is important first in suggesting a closer relationship with a Chinchilla species than any other zygomaticurine, and secondly in demonstrating differences which may be interpreted as indicating it could be ancestral to the Chinchilla species.

The importance of zygomaticurines in correlation has been suggested by Stirton, Tedford and Woodburne (1968), and they may be useful in interpreting the age of the Chinchilla Sand relative to other late Tertiary mammal bearing deposits.

Euryzygoma sp.
(Plate 58a)

The most common diprotodontid from the Allingham Formation is referable to the nototheriine genus *Euryzygoma*. Only one species is named, *E. dunense*, from the Chinchilla Sand.

The Allingham *Euryzygoma* is represented by one complete (F7891) and two partial skulls as well as several dentaries and isolated teeth. If it were not for the enormous variation apparently exhibited by *E. dunense* from Chinchilla, it would be tempting to believe that more than one species was represented by the Allingham remains. This may yet prove to be the case. The possibility that there is more than one Chinchilla species is also under examination. Until this problem is resolved, the specific identity of the Allingham *Euryzygoma* must remain uncertain.

Although premolar morphology can be matched in the two samples (e.g. F7765 from Allingham, and some of the teeth included in F5812 from Chinchilla), several cranial differences include morphology of the zygomatic arch which in the Allingham *Euryzygoma* more closely resembles less specialized nototheriines than does *E. dunense*.

NOTOTHERIINE, genus indet.
(Plate 58b-c)

A small nototheriine is represented by several dentary fragments including F7766, an isolated worn RP⁴; F7830, a maxillary fragment of an as yet unprepared skull containing M³⁻⁴. This animal differs from the Allingham *Euryzygoma* in being much smaller, having a very reduced M⁴ with markedly narrow metaloph, and in several characters of the dentary.

It resembles in molar and dentary morphology several specimens from Chinchilla regarded previously as *Euowenia grata*, a form whose generic

status is in doubt. M⁴ of F519 (holotype of *Euowenia grata*) from Chinchilla is similar but has a wider metaloph than the Allingham specimen.

Taxonomic assessment of this small Allingham nototheriine will have to await preparation of the skull.

INCERTAE SEDIS
(Plates 55d-f, 57g)

A single tooth fragment (F7792) may represent an otherwise unknown family. It represents a medium to large-sized animal, presumably marsupial, that has a well-developed cingulum, and at least two small twinned cusps. Twinned cusps are rare in marsupials. They occur in some perameloids (e.g. *Macrotis*) and phascolarctids.

Coprolites (e.g. F7761) are common in the deposit. Size and shape suggest they were produced by a medium to large-sized animal, possibly a corcodilian, large snake, or diprotodontid, and that they were deposited in water. Some of the largest are too massive to have maintained their shape had they been deposited on hard ground or transported. Further, they bear no impressions such as might be expected if they were deposited on an irregular terrestrial surface.

DISCUSSION

At this stage in our knowledge of the Bluff Downs local fauna, twenty-two taxa including thirteen mammals have been recognized. There is no representation of monotremes, dasyurids, thylacinids, thylacomyids, phalangerids, petaurids, burramyids, myrmecobiids, wynyardiids, notoryctids, or tarsipedids. Except for the last four, all are represented in older as well as younger deposits and their absence from the Bluff Downs local fauna cannot be the result of absence from the Australian continent at that time. In some families, representative modern forms occur in most broad ecological habitats so that absence of monotremes, dasyurids, petaurids, and burramyids may be the result of chance sampling. Notoryctids, myrmecobiids and thylacomyids are represented in the modern fauna by arid-adapted forms, most of which are rare, and their absence from the Bluff Downs local fauna may reflect a similar Pliocene rarity or an unsuitable environment.

ASPECTS OF THE PALAEOENVIRONMENT

Accuracy of interpretation depends on both extent to which the sample represents the contemporaneous fauna in diversity and species abundance, and extent that ecological requirements of

fossil forms may be interpreted from those of their nearest living relatives. Major uncertainties remain.

Certainties are that *Chara*, crustaceans, and fish indicate persistent fresh water, and tortoises, crocodiles and Black-headed Storks are supporting evidence for at least seasonal bodies of water. Modern tortoises and crocodiles can migrate considerable distances to find suitable water and therefore are not evidence for permanent water. When the modern Allingham Creek is running, small fish are abundant and tortoises common. When the creek is not running tortoises form a relatively much larger part of the biomass in waterholes (pers. comm. J. Barratt), presumably a reflection of their ability to migrate.

Among carnivores known from the fossil fauna, the dog-sized *Thylacoleo* is the largest mammalian carnivore. The crocodile *Palimnarchus* was probably capable of killing any of the mammals represented in the fauna. Although tortoises could have formed at least part of the food supply of *Palimnarchus*, not one of the hundreds of plates preserved show evidence of tooth marks which would suggest such predation. Further, there are very few fish remains in the deposit, suggesting they were not an abundant source of crocodile food. It is possible that *Palimnarchus* hunted mainly mammals (and/or birds), either waiting for them to come to water, or possibly even pursuing them near shore.

Mammals represented in the deposit suggest arboreal (*Koobor jimbarratti*) as well as terrestrial habitats. The much greater abundance of terrestrial forms suggests that the surrounding area was savannah woodland. Terrestrial forms include numerous grazing kangaroos and diprotodontids, including a species of *Protemnodon* which may have been a browser. There is evidence from macropodid post-cranial remains of a Tree Kangaroo-like form which may have been the same species of *Protemnodon*. Considering the apparently rapid evolution and radiation of kangaroos in the late Tertiary (Bartholomai 1972), it is perhaps particularly unwise to extrapolate to these lower Pliocene forms, habitat requirements of supposedly similar modern forms. Thus, *Macropus* (*Osphranter*) cf. *M. woodsi* may not resemble most modern members of the subgenus *Osphranter* in showing any preference for rocky hills or slopes.

In summary, there is evidence to suggest that bodies of water were present for at least months at a time. It is also probable that these lakes, rivers, or swamps were not permanent. It is possible that the Bluff Downs local fauna represents a riparian assemblage.

COMPARISON WITH OTHER KALIMNAN AND POST KALIMNAN LOCAL FAUNAS

Comparisons of the Bluff Downs local fauna should be made with the Chinchilla, Hamilton, Awe, Fisherman's Cliff, Kanunka, Palankarinna, and Beaumaris local faunas. This comparison is summarized in Table 1 where only species occurring in the Bluff Downs local fauna are considered.

CHINCHILLA: Except for the peramelid, all Bluff Downs mammal species are closely comparable with forms from the Chinchilla local fauna of southeastern Queensland. Frequently the Bluff Downs member of each species pair is structurally ancestral in terms of size and morphology. For this reason, differences between the two local faunas are not regarded here as evidence of merely ecological or geographical differences, but rather as evidence for a difference in age, with Chinchilla appearing to be the younger of the two. We support the suggestion of Bartholomai (1973) of a late Pliocene age for Chinchilla. It is not likely to be Pleistocene because of the closer similarities of Chinchilla species to those of Bluff Downs than to those from eastern Darling Downs Pleistocene deposits. For example, there is no undoubted record of *Diprotodon*, *Nototherium*, *Procoptodon*, *Fissuridon*, *Macropus* (*Macropus*), or *Sarcophilus* from Chinchilla or Bluff Downs, nor is there any record of *Euryzygoma*, *Macropus* cf. *M. dryas* or *Protemnodon* cf. *P. chinchillaensis* from eastern Darling Downs deposits.

HAMILTON: The Pliocene Hamilton local fauna of Victoria (Turnbull and Lundelius 1970) is not broadly comparable with either the Bluff Downs or the Chinchilla local faunas since it contains mostly small mammals represented by isolated teeth. Only *Palorchestes* near *P. painei* appears to suggest that Hamilton is structurally older than Chinchilla which contains *P. parvus*. Teeth from the Hamilton deposit came from a soil overlain by a basalt dated at 4.35 ± 0.1 Myr (Turnbull and Lundelius 1970). Therefore the Hamilton local fauna may be closely comparable in age to the Bluff Downs local fauna.

AWE: The Pliocene Awe local fauna of Papua (Plane 1967) contains two structurally simple species of *Protemnodon* and in this respect they resemble Bluff Downs and Chinchilla species. Awe zygomaturines (*Kolopsis rotundus* and *Kolopsoides cultridens*) are structurally more primitive than the Bluff Downs *Zygomaturus*, and clearly resemble late Miocene Alcoota zygomaturines. However, the Awe nototheriine (*Nototherium watutense*) is not very different from the Bluff Downs nototheriines (*Euryzygoma* and *Euowenia*). Lack of a

TABLE 1: THE DISTRIBUTION OF ELEMENTS OF THE BLUFF DOWNS LOCAL FAUNA IN OTHER LATE TERTIARY AND EARLY QUATERNARY LOCAL FAUNAS

Bluff Downs local fauna	E. Darl. Downs	Kanunka	Fisherman's Cliff	Chinchilla	Hamilton	Awe	Palankarina	Beaumaris
crustacean		s?					s?	
fish (teleost)	s?	s?	s?	s?			s?	
? <i>Chelodina</i> sp.	s?	s?	?	s?				
<i>Palimnarchus</i> sp.		f		s?		f	f	
cf. <i>Amphibolurus</i> sp.								
<i>Varanus</i> sp.	s?	f		s?				
? elapid								
boid						s?		
<i>Xenorhynchus asiaticus</i>	c	c	c	c		c	c	
<i>Perameles allinghamensis</i>					g?		sf	
<i>Phascolonius lemleyi</i>	g	s?	f	g				
<i>Koobor jimbaratti</i>				g				
<i>Thylacoleo</i> sp.	g	g		g				
<i>Protemnodon</i> sp.	g	s?	g	g	s?	g		
<i>M.</i> (<i>Prionotemnus</i>) cf. <i>M. dryas</i>	sg	sg	sg	s?			sg	
<i>M.</i> (<i>Osphranter</i>) cf. <i>M. woodsi</i>	sg		sg	s?				
small macropodid, cf. <i>Thylagale</i>					s?			
small macropodid, gen. indet.								
<i>Zygomaturus</i> sp.	g	g?	g	s?		sf	g	g
<i>Euryzygoma</i> sp.				g				
nototheriine, gen. indet.	g?	g		s?		sf	sf	
Maximum number of mammal species in common	0	2?	0	4?	2?	0	0	0

Abbreviations: s, either same species or else not yet demonstrated to be a different species; sg, same subgenus; g, same genus but different species; sf, same subfamily; f, same family; c, same class.

premolar referable to *N. watutense* prohibits close comparison, but it is clear that all three forms are broadly similar. Anderson (1937) compares the holotype with known nototheriines and concludes it is closest in size to *Euowenia grata*. Considered as a whole, the Awe zygomaturines suggest that the Awe local fauna is structurally older than the Bluff Downs local fauna although Page and McDougall (1972) suggest that a date of 3.1 Myr may be the oldest reliable date associated with the Awe local fauna. Plane (1967) reports dates between 5.7 and 7.6 Myr for intercalated pyroclastics.

FISHERMAN'S CLIFF: Marshall (1973) regards the Fisherman's Cliff local fauna to be probably late Pliocene or early Pleistocene in age. The macropodids include a species of *Protemnodon* which Marshall considers is most similar to *P. devisi* (as *P.* cf. *P. otibandus*) from Chinchilla. The specimen is not figured. The diprotodontids include a possible species of *Diprotodon* which suggests this local fauna is Pleistocene in age.

KANUNKA: The Kanunka local fauna from the Lake Eyre Basin of South Australia is briefly

described by Stirton, Tedford and Miller (1961) who consider it to be ?Pleistocene in age. Their preliminary comments suggest similarity to the Bluff Downs local fauna, but do not exclude comparison with Pleistocene deposits such as those from the eastern Darling Downs. The apparent absence of *Diprotodon* favours a late Pliocene age, although it is probably younger than the Bluff Downs or Chinchilla local faunas.

PALANKARINNA: Stirton, Tedford and Woodburne (1968) regard the Palankarina local fauna from the Lake Eyre Basin of South Australia to be late Pliocene in age. Faunal diversity is low. The perameloid (*Ischnodon australis*) is a thylacomyid and hence not comparable with *Perameles allinghamensis*. Diprotodontids include the nototheriine *Meniscolophus mawsoni* and the zygomaturine *Zygomaturus keanei*. It is apparent that generic boundaries of *Meniscolophus*, *Euryzygoma* and 'Euowenia' need re-examination. However, *M. mawsoni* appears to differ specifically from Chinchilla and Bluff Downs nototheriines. *Z. keanei* and the *Zygomaturus* from Bluff Downs differ at

what is probably a specific level, but it is not yet possible to assess which form is structurally ancestral to the other. Bartholomai (1975) has recently recognized the Palankarinna macropodid *Prionotemnus palankarinnicus* from Chinchilla.

BEAUMARIS: Stirton, Tedford and Woodburne (1968) review the Beaumaris local fauna from southern Victoria, considering it to be early Pliocene in age. *Zygomaturus gilli* is, like *Z. keanei* and *Z. trilobus*, unlike the Bluff Downs *Zygomaturus* which resembles, but differs from, the Chinchilla *Zygomaturus*. Zygomaturine taxonomy and biostratigraphy is in need of careful re-examination and at this stage it does not enable us to assess the relative ages of the two local faunas.

In summary, the Bluff Downs local fauna compares most closely with the Chinchilla local fauna but may prove to be also similar in composition to the Kanunka and Hamilton local faunas. Apparent differences between these and other Kalimnan local faunas may be the result of differing ages, latitudes, conditions of accumulation, or ecological setting.

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photographs used in the plates. Mrs E. Archer prepared the holotype of *Phascolonus lemleyi*, and Mr A. Elliot prepared the skull of *Euryzgoma* sp. (Plate 58a) and the dentary of the small nototheriine (Plate 58c).

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PLATE 54

Bluff Downs invertebrates and lower vertebrates

- a. F7772 teleost vertebra
 - b. F7771, teleost spine
 - c. F7767, vertically fluted crocodile tooth
 - d. F7763, tooth of *Palimmarchus* sp.
 - e. F7764, tooth of *Palimmarchus* showing occlusal wear of tip
 - f. F7829, crustacean gastrolith
 - g. F7826, small snake vertebra, possibly elapid
 - h. F7813, tooth possibly referable to *Varanus* sp.
 - i. F7812, fragment of an agamid dentary
 - j. F7774, vertebra of *Varanus* sp.
 - k. F7775, vertebra of a large boid
- Unless otherwise indicated, line represents one cm.

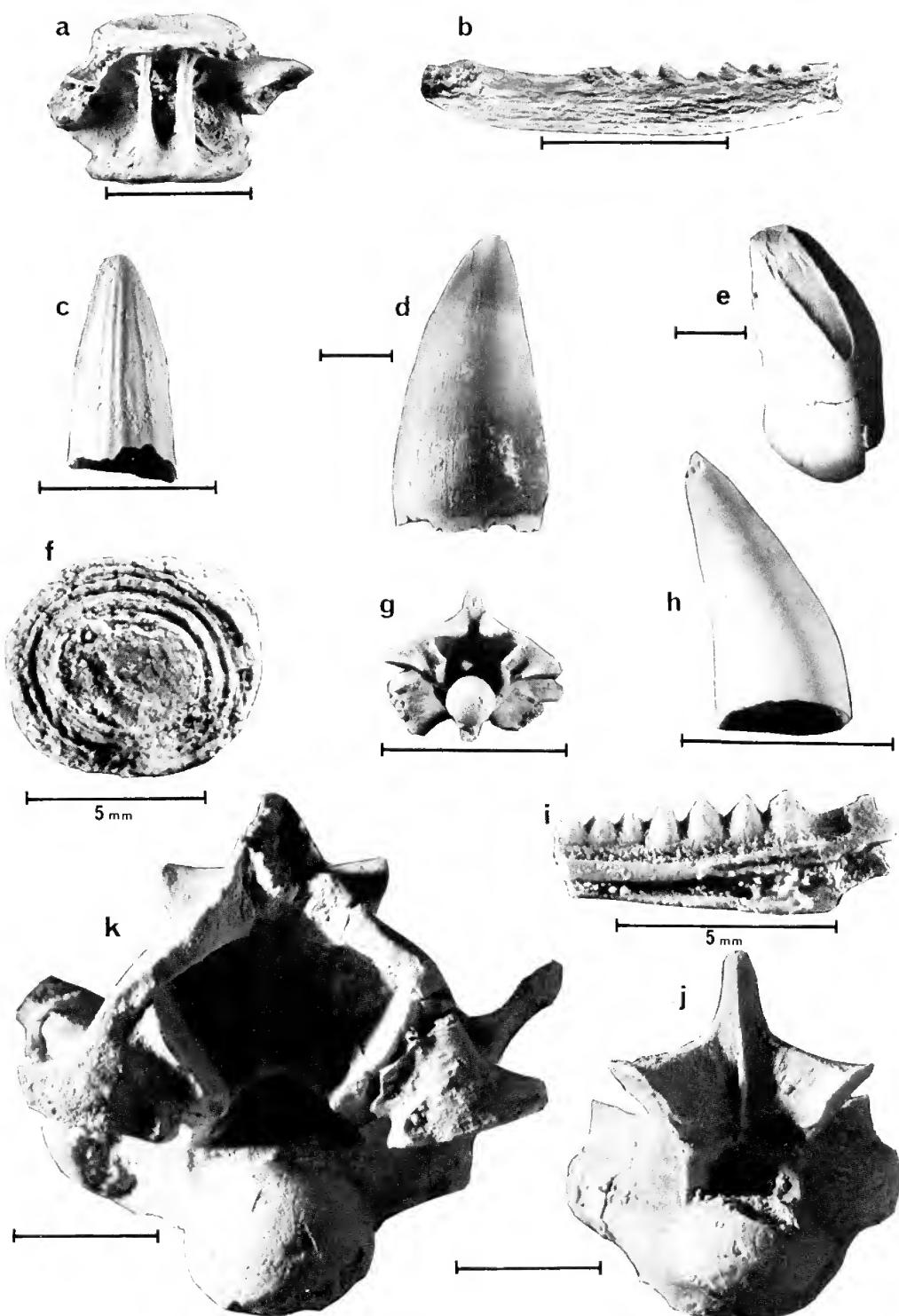


PLATE 55

Bluff Downs mammals

- a, F7762, right dentary of *Thylacoleo* sp. with broken P_4 and M_1
b, F7822, stereopair scanning electron microscope photographs, RM^1 or RM^2 , holotype *Koobor jimbarratti* n. gen. and sp.
c, F7821, stereopair scanning electron microscope photographs, RM^2 , holotype *Perameles allinghamensis* n. sp.
d-f, F7792, stereopair, tooth fragment of unknown type of mammal

Line represents one cm.

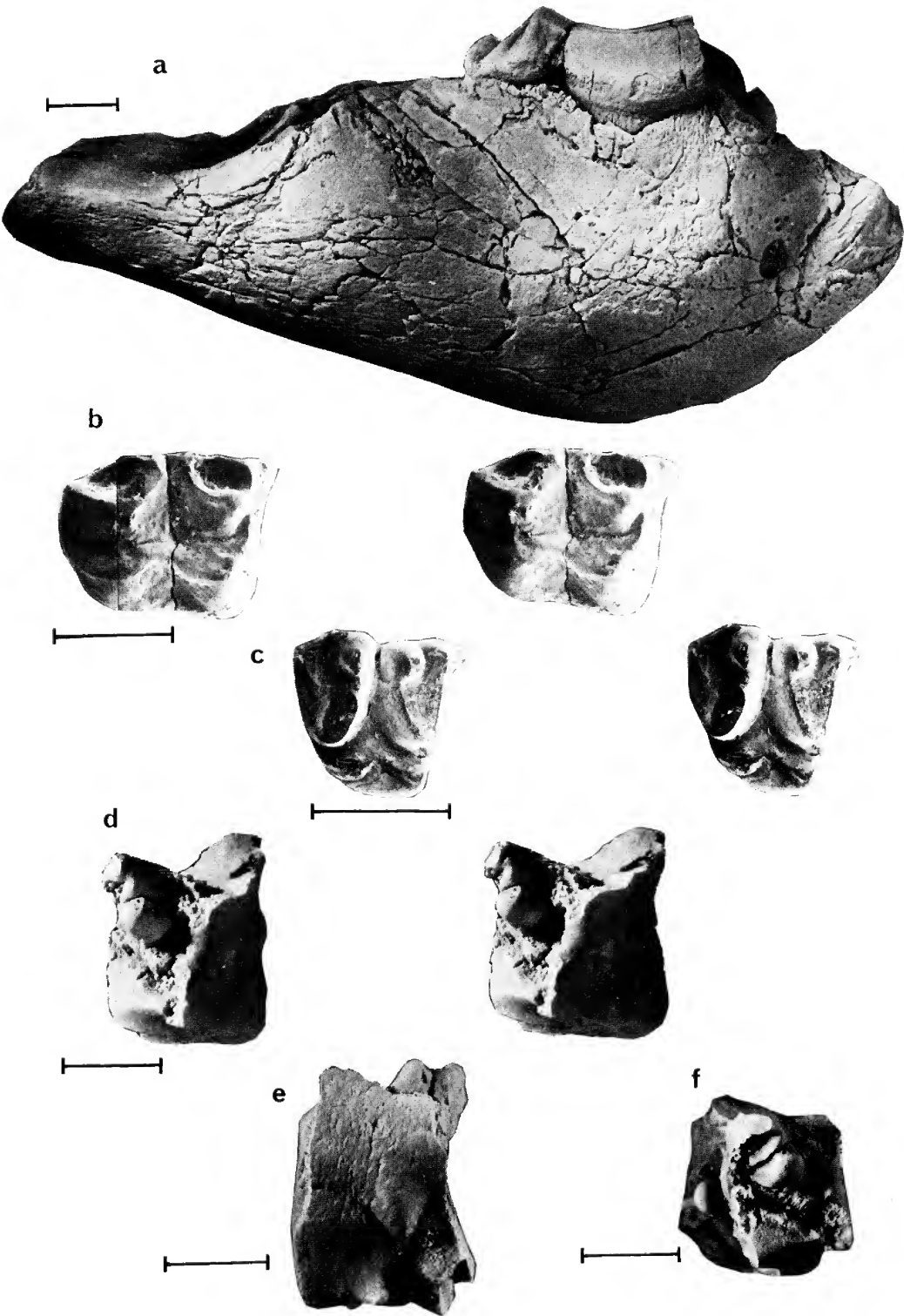


PLATE 56

Phascolonus lemleyi n. sp.

a, F7818, LI₁, lingual view

b-d, F7819, left dentary, holotype, *Phascolonus lemleyi* n. sp.

Line represents one cm.

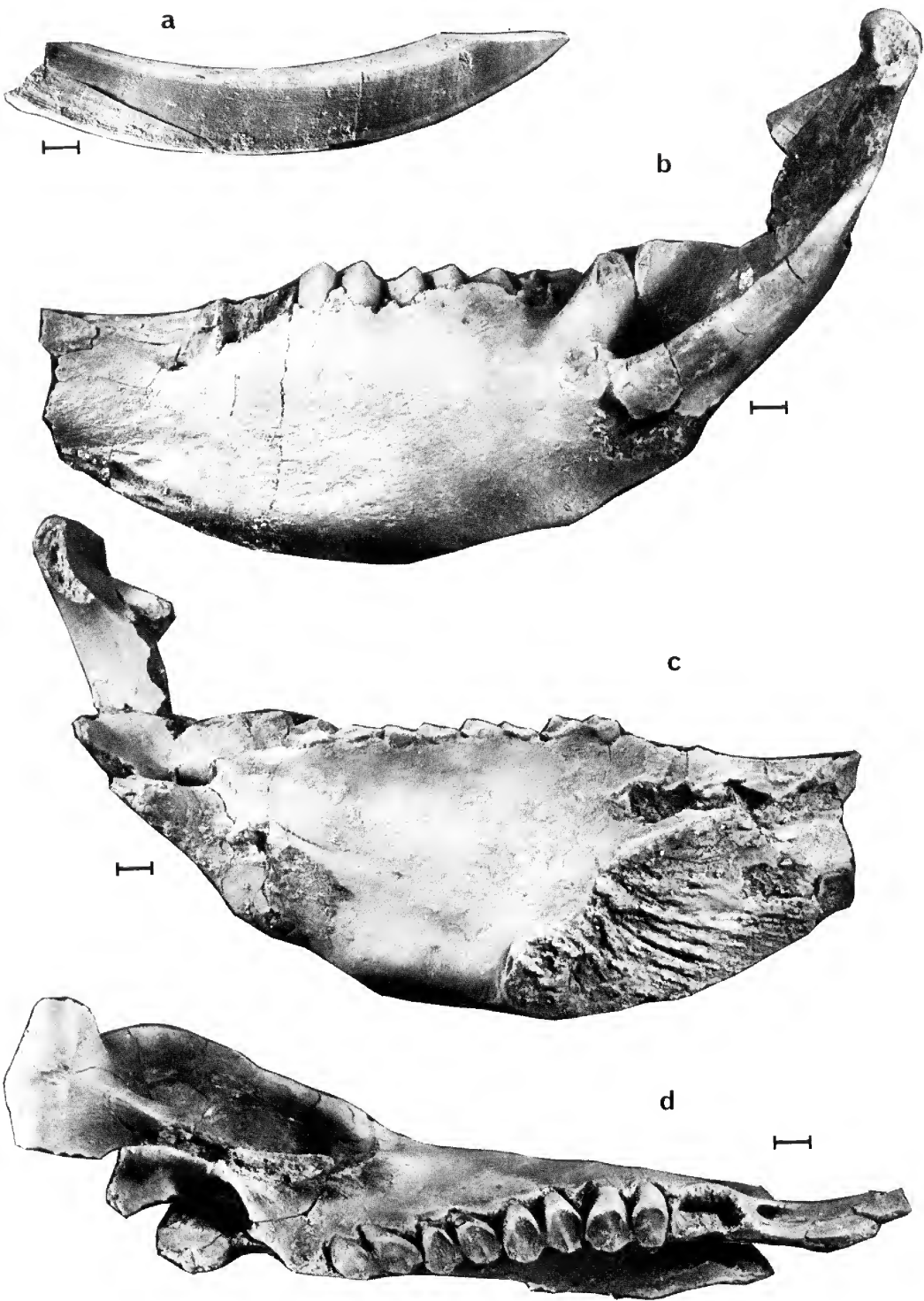


PLATE 57

Bluff Downs macropodids and coprolite

- a, F7810, right maxillary fragment with parts of RM^{1-2} and M^{3-4} , *Protemnodon* sp.
 - b, F7812, right dentary fragment with $RdP_4 - M_1$, *Protemnodon* sp.
 - c-d, F7823, right dentary with RP_3 , dP_4 , M_1 , and P_4 (excavated, d), *Macropus* sp. cf. *M. dryas*
 - e, F7785, isolated upper molar, *Macropus (Osphranter)* sp., cf. *M. woodsi*
 - f, F7784, isolated lower molar, small macropodine of uncertain affinities
 - g, F7761, coprolite
- Line represents one cm.

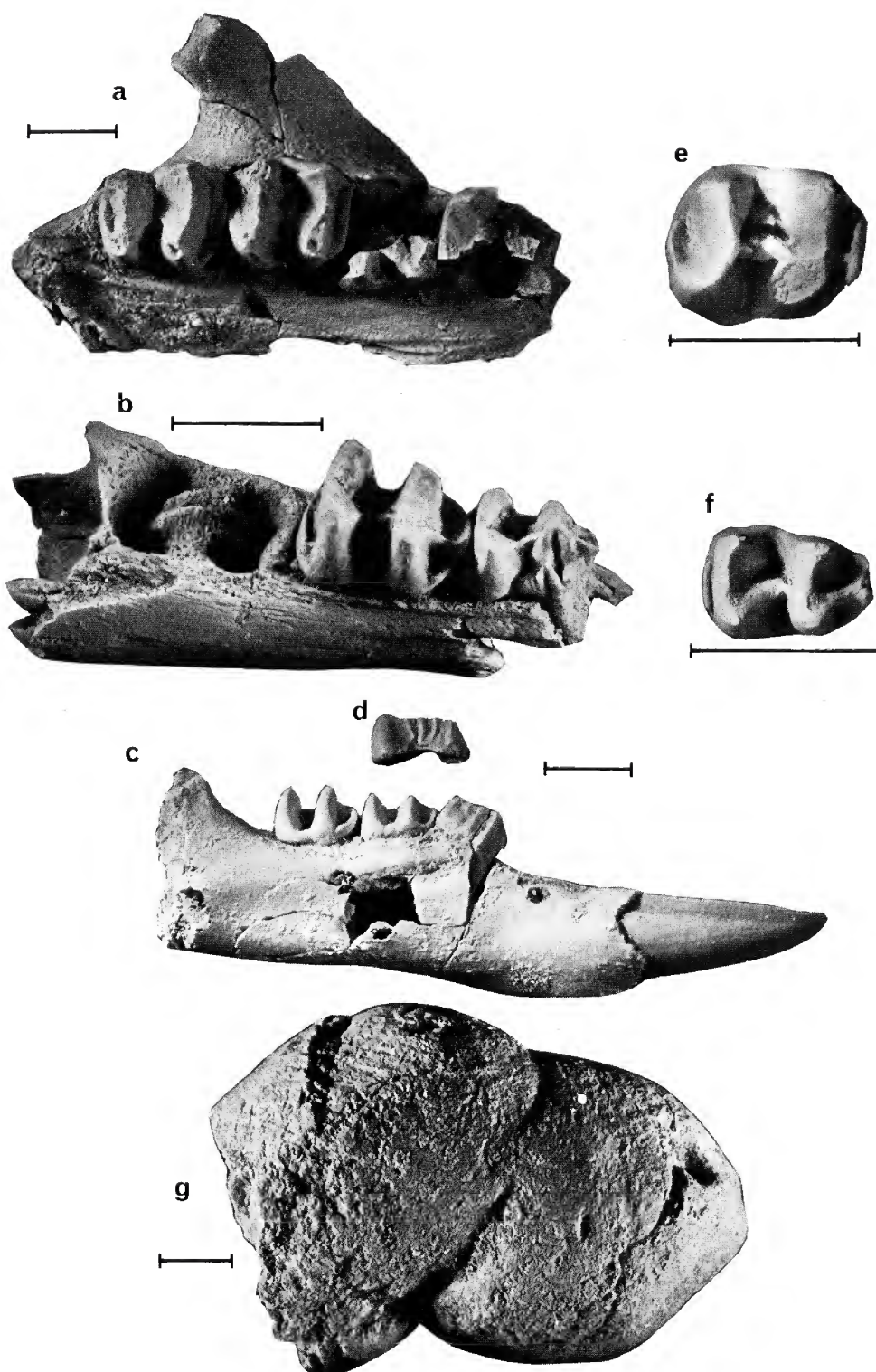
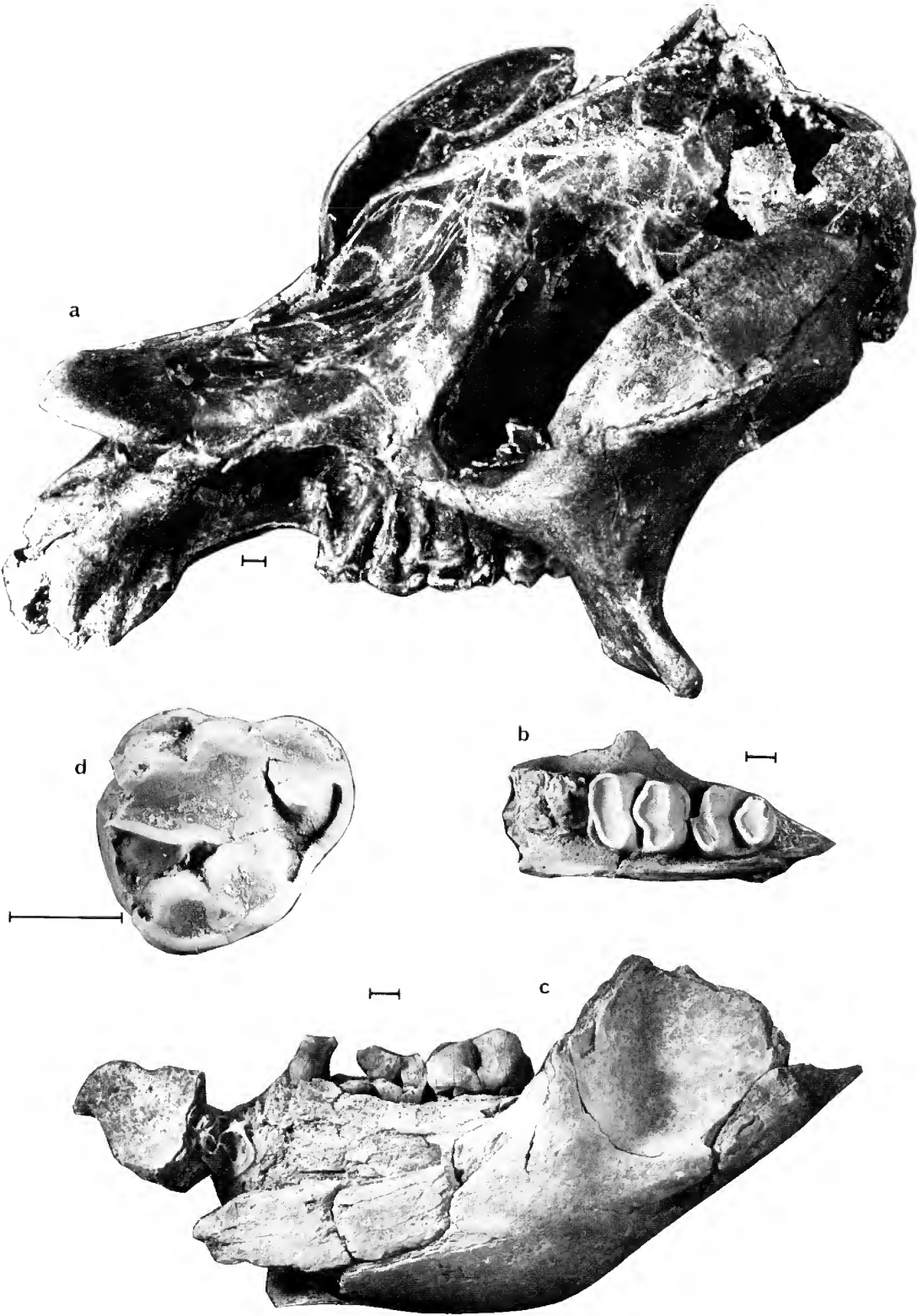


PLATE 58

Bluff Downs diprotodontids

- a, F7891, skull, *Euryzygoma* sp.
 - b, F7830, left maxillary fragment, small nototheriine
 - c, left dentary fragment with damaged LM₂₋₄, small nototheriine
 - d, F7776, isolated RP⁴, *Zygomaturus* sp.
- Line represents one cm.





DARDURUS, A NEW GENUS OF AMAUROBIID SPIDER FROM EASTERN AUSTRALIA, WITH DESCRIPTIONS OF SIX NEW SPECIES

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ABSTRACT

A new genus *Dardurus* (fam. Amaurobiidae) is described, with six new species *D. spinipes*, *D. silvaticus*, *D. tamborinensis* (cribellate), *D. nemoralis*, *D. saltuosus* and *D. agrestis*. The cribellum looks like a flat semi-circular colulus and a magnification of 200x was needed to see the spinning areas. The species show a reduction in the number of spinning tubes with a corresponding reduction in the length and number of hairs in the calamistrum until in *D. tamborinensis* neither spinning tubes nor calamistrum are present. The spiders live a sedentary life in small, decorated silk tubes with two openings. Scanning electron micrographs of the cribella of *Ixeuticus longinquus* (Koch, L., 1867) and *Stiphidion facetum* Simon, 1902 are included for comparison.

In the latter half of the nineteenth century collections of spiders were made around the sea ports of Queensland and New South Wales for the Godeffroy Museum, Hamburg. About 600 spiders were described in *Die Arachniden Australiens* and its *Supplement* by Koch (1871-81) and Keyserling (1881-89). At about the same time Thorell described 46 species from Cape York Peninsula in *Studi sui Ragni Malesi e Papuani*, vol. 3. Between 1893 and 1920 Rainbow contributed much to the knowledge of Australian spiders. He was entomologist at the Australian Museum, Sydney for many years and not only described about 200 spiders but also wrote much on their webs and behaviour. In 1911 he published a *Census of Australian Araneidae* where he listed approximately 1200 species. Included among these were 100 spiders described by Hogg from specimens in the British Museum. From 1926 Hickman, Australia's foremost araneologist, described about 70 spiders most of which were from Tasmania and some of which required the erection of new families. Recently Main has revised and re-defined some of the mygalomorph genera. It will be seen from this brief review that the araneomorphs of E. Australia have been rather neglected since 1920, so it is not surprising that a new genus, like *Dardurus*, can be found in a suburban garden.

The term 'amaurobiid' is used in the broad sense of Lehtinen (1967) not in the restricted sense of Forster and Wilton (1973). All specimens have

been deposited in the Queensland Museum (QM). Measurements of the cephalothorax length (CL), cephalothorax width (CW), abdomen length (AL), abdomen width (AW), and measurements of leg segments were made with an ocular micrometer and converted to millimetres.

Dardurus nov. gen.

Small size. Both rows of eyes straight if viewed from above, procurved if viewed from front; anterior median eyes smallest. Cheliceral boss present. Labium wider than long. Maxillae narrow at base, wide and truncated at apex with well marked serrula and scopula. Sternum widely truncate, produced posteriorly between fourth coxae. Trochanteral notch absent. Anterior tibiae with more than 3 pairs of conspicuous long ventro-lateral spines. Superior tarsal claws with 7 pectinations; inferior claw smooth. Palpal tarsus longer and wider than other tarsi. Plumose hairs absent. Trichobothria in a single row of increasing length distally on metatarsi and tarsi, irregularly placed on tibiae. Trichobothria on cymbium. Six spinnerets, anterior laterals largest. Undivided cribellum or flat semicircular colulus. Cribellum absent in ♂. Calamistrum proximal or absent. Epigynum with undivided fossa. Apophyses on patella and tibia of ♂ palp. Embolus curved, spiniform; conductor membranous. Four unbranched tracheal tubes arising from a median posterior

spiracle. The spider lives on the underside of logs or in soil in a camouflaged silken tube with two openings.

The generic name is derived from the Aboriginal work 'dardur'—a bark hut.

TYPE SPECIES: *Dardurus spinipes* n. sp.

***Dardurus spinipes* n. sp.**

(Figs. 1–10, 19a; Plates 59A, 60B)

MATERIAL EXAMINED

HOLOTYPE: Open sclerophyll forest on Brisbane River, Roedean St, Fig Tree Pocket, Brisbane, SE.Q., V. Davies, 22.v.74, ♂, QM W4877.

PARATYPES: Open sclerophyll forest on Brisbane R., Roedean St, Fig Tree Pocket, Brisbane, SE.Q., V. Davies, 15.vi.74, 1♂, QM W4878; 4.iii.74, 1♀, 1 juv., QM W4879; 21.i.73, 1♀, QM W4880; 12.viii.73, 1♀, 1♂, QM W4881; 9.ix.73, 3♀, QM W4882; 2.viii.73, 2♀, 1♂, 1 penult. ♂, 1 juv., QM W4883; 22.v.74, 3♀, 4♂, 1 juv., QM W4884; 15.vi.74, 2♀, 1♂, QM W4885; 15.vi.74, 1♀, QM W4886; 1.viii.74, 3♀, QM W4887. Under log in bank near Little Yabba Creek, Conondale Ra., SE.Q., R. Raven, 31.viii.74, 6♀, 1♂, QM W4888; 31.viii.74, 4♀, 2 juv., QM W4889.

DESCRIPTION OF FEMALE

CL 1.50; CW 0.98; AL 1.78; AW 1.10.

Cephalothorax and legs are orange brown, abdomen is grey-black with lighter grey pattern (Figs. 1, 2). Small white patches ('thoracic patches') one on each side of the thoracic fovea similar to those noticed by Forster and Wilton (p. 166, 1973) in some of the female cribellate *Amphinectidae* from New Zealand. The long spines on tibiae and metatarsi I and II are reddish brown in colour.

Both rows of eyes are procurved if viewed from the front, straight if viewed from above (Figs. 3a, b). The ratio of eyes AME:ALE:PME:PLE is 6:10:9:9. There are 4 teeth on retromargin of chelicerae; 2 large and 3 small teeth on promargin (Fig. 4). The maxillae are narrow at the base, wide and truncated at the apex with a well marked serrula and scopula. The labium is wider than long in ratio 1:0.63. The sternum is longer than wide, 1:0.87.

Notation of spines: Palp: tibia, p. 1–2.2; tarsus, numerous spines (Fig. 5). First leg (Fig. 6): femur, d.1.p.1. distal; tibia, v.2.p.0.1.1.1.1.(1).r.0.1.1.1.1; metatarsus, v.1.p.0.1.1.1.r.0.1.1.1; tarsus, 0. Second leg: femur, d.1.1.0; tibia, v.2.p.0.1.(1).1.1.r.0.1.0.1.1; metatarsus, d.1.1.0.0.p.1.1.1.1.r.0.1.1.1. Third leg: tibia, d.0.1.0.v.1.0.1.p.1.1.0.r.1.1.0; metatarsus, numerous small spines. Fourth leg: tibia, v.1.0.1.0.2.p.0.1.0.1.0.r.0.1.0.1.0; metatarsus, several spines. Calamistrum proximal, consisting of 7 rather sparse curved hairs (Fig. 7). Superior tarsal claws with 7 pectinations (Fig. 8); the inferior claw smooth.

Six spinnerets: anterior laterals (AS) largest, in ventral view tending to obscure the rest. AS:cribellum, 1:1.10. The cribellum has the appearance of a large flat colulus. The electron scanning microscope shows spinning tubes are present in 6 transverse alternating rows with about 15–16 tubes in each row (Plate 60, B). The epigynum (Figs. 9a, b, 19a) occupies a large part of the ventral abdominal surface and has well marked lateral ridges. The fossa is undivided, i.e. there is no median ridge or guide. Width of external epigynum $2\frac{1}{2} \times$ length.

VARIATION: Cephalothorax lengths were from 1.14–1.50. Sometimes there are 2 large and only 2 small teeth on the promargin of the chelicerae. There was some variation in the arrangement of spines on the corresponding legs from left and right sides of the spiders. This is indicated by the use of () in the notation of spines. An extra prolateral spine is not uncommon on the first and second tibia. The spiders from Conondale Range were darker in colour and there was a dorsal spine on the fourth femur.

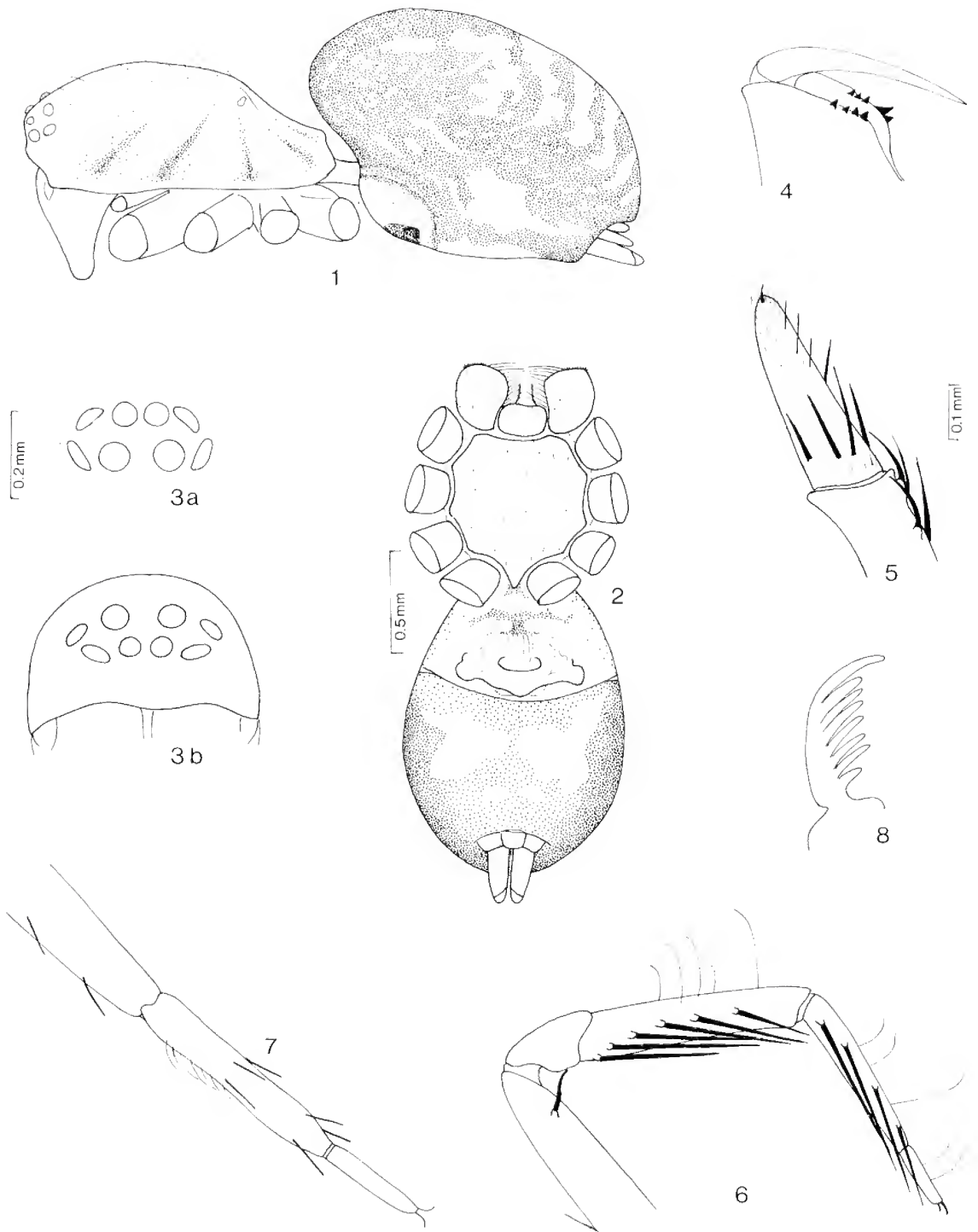
DESCRIPTION OF MALE

QM W4878: CL 1.20; CW 0.80; AL 1.32; AW 0.88.

Cephalothorax lengths varied from 1.02 to 1.46 mm. Males are similar to females in colour, general structure and spination of the legs except that the

TABLE 1: LEG MEASUREMENTS OF *D. spinipes* ♀ AND (♂)

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
i	1.06(0.98)	0.46(0.40)	1.00(0.96)	0.82(0.80)	0.28(0.34)	3.62(3.48)
ii	0.84(0.74)	0.42(0.36)	0.66(0.60)	0.66(0.64)	0.26(0.26)	2.84(2.60)
iii	0.68(0.62)	0.36(0.30)	0.38(0.40)	0.56(0.52)	0.24(0.24)	2.22(2.08)
iv	0.94(0.90)	0.42(0.34)	0.72(0.74)	0.84(0.80)	0.30(0.30)	3.22(3.08)
palp	0.40(0.42)	0.20(0.14)	0.28(0.20)	—	0.42(0.66)	1.30(1.42)



FIGS. 1-8: *D. spinipes*. 1, lateral view; 2, ventral view; 3a, eyes from top; 3b, eyes from front; 4, chelicera; 5, tarsus of palp; 6, first leg; 7, fourth leg; 8, superior tarsal claw.

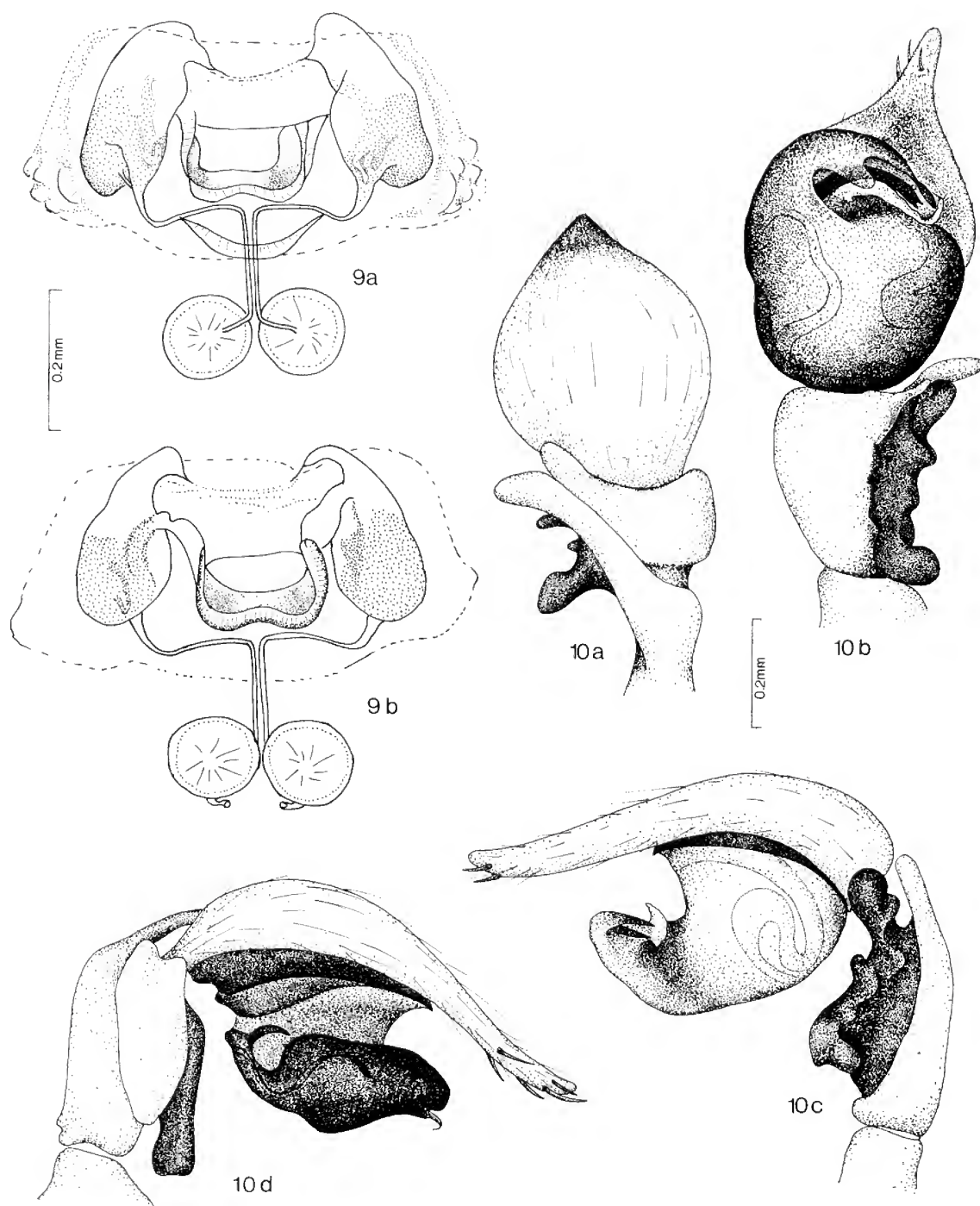


FIG. 9: ♀ *D. spinipes*. 9a, external epigynum, cleared; 9b, internal epigynum.

FIG. 10: ♂ *D. spinipes*. 10a, palp, dorsal; 10b, palp, ventral; 10c, palp, retrolateral; 10d, palp, prolateral.

prolateral distal spine on femur I is absent and there are no 'thoracic patches' near the fovea. There is a colulus in the penultimate and mature ♂. It is smaller than the ♀ cribellum and has no spinning tubes. Neither the penultimate nor the mature male has a calamistrum. Trichobothria are present on the cymbium. The palp has a finger-shaped anterior retrolateral apophysis on the patella and a very complex one with several protuberances on the retrolateral surface of the tibia (Fig. 10a, b, c). An apophysis arises from the tegulum and curves over the embolus which is retrolateral to the apophysis. A small ventral flange on the latter appears to keep the embolus in place. The spiniform embolus rests on a membranous conductor. Whether the apophysis is a median apophysis or whether this is absent is uncertain.

HABITS AND LIFE HISTORY

All the spiders were collected from open sclerophyll forest. They live in small (10–13 mm) tubes with 2 openings (Plate 59A) and are found on rotting wood or sometimes under stones or in soil. The tube which is decorated with bark debris (hence the generic name) or soil particles has no web outside it. Females were found throughout the year; penultimate males from February until May and males till the end of August. Males were often found with one palp broken off and it was not unusual to find them occupying the same tube as females. Egg sacs containing 3–6 eggs were found from August to March.

Dardurus silvaticus n. sp.

(Figs. 11–13, 19c; Plates 59B, 60A)

MATERIAL EXAMINED

HOLOTYPE: Rain forest, Mt Glorious, 32 km NW. Brisbane, SE.Q., V. Davies, 19.vii.74, ♀, QM W4890.

PARATYPES: Rain forest, Mt Glorious, SE.Q., V. Davies, 19.vii.74, 1♂, QM W4891; 20.vi.74, 2♀, 1♂, QM W4892.

DESCRIPTION OF FEMALE

CL 1.18; CW 0.88; AL 1.28; AW 1.10.

The spider is similar in colour and pattern to *D.*

spinipes however the abdominal pattern shows an extension of the pale patches over the posterior half of the abdomen giving it a lighter colour (Fig. 11). Small 'thoracic patches' are present. The eyes are similar to *D. spinipes*. There are 4 teeth on the retromargin of the chelicerae. The labium is wider than long 1.0:66. Sternum longer than wide 1.0:91.

Notation of Spines: Palp: tibia, p.1.2; tarsus, numerous small spines, First leg femur, d.1.1(1).0. p.1. distal; tibia, v.2.p.0.1.1.1.1.r.0.1.1.1.1(1); metatarsus, v.1.p.0.1.1.1.r.0.1.1.1; tarsus, 0. Second leg: femur, d.1.1.0; tibia, v.2.p.0.1.1.1.1. r.0.1.0.1.1; metatarsus, d.1.1.0.0.p.1.1.1.1.r.0.1.1.1. Third leg: tibia, d.0.1.0.v.1.0.1.p.1.1.0.r.1.1.0; metatarsus, numerous small spines. Fourth leg: tibia, v.1.1.1.0.1.p.0.1(1).0.1.0.r.0.1.0.1.0; metatarsus, several spines. Calamistrum, proximal and well developed consisting of 9 curved hairs. Ratio of AS:cribellum 1:1.18.

The cribellum has about nine rows of spinning tubes with at least 25 tubes in a row (Plates 59B, 60A) which is many more than *D. spinipes*. In both species the tubes are unsegmented. The epigynum (Figs. 12a, b, 19c) is less chitinized than *D. spinipes* with weak lateral ridges and a large open fossa almost the width of the epigynum.

VARIATION: Cephalothorax of ♀ QM W4892 is 1.28 mm long. As in *D. spinipes* there may be extra spines on the first and second tibiae.

DESCRIPTION OF MALE

QM W4891: CL 1.10; CW 0.78; AL 1.12; AW 0.74.

The colour and pattern is similar to ♀. There are no 'thoracic patches' on the cephalothorax.

Notation of Spines: First leg: femur, d.1.0.p.1. distal; tibia, v.2.p.0.1.1.1.1.r.0.1.1.1.1; metatarsus, v.1.p.0.1.1.1.r.0.1.1.1; Second leg: femur, d.1; tibia, v.2.p.0.1.1.1.1.r.0.1.0.1.1; metatarsus, d.1.1.0.0. p.1.1.1.1.r.0.1.1.1. Third leg as in female. Fourth leg: tibia, v.1.0.1.0.1.p.0.1.0.0.r.0.1(1).0.1.0. There is no calamistrum.

Male palp: The tibial apophysis on the palp (Fig. 13a, b) is less complex than *D. spinipes* with fewer

TABLE 2: LEG MEASUREMENTS OF *D. silvaticus* ♀ AND (♂)

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
i	0.84(0.88)	0.40(0.40)	0.72(0.86)	0.64(0.76)	0.26(0.32)	2.86(3.22)
ii	0.66(0.70)	0.34(0.34)	0.52(0.54)	0.52(0.60)	0.22(0.28)	2.26(2.46)
iii	0.52(0.58)	0.28(0.28)	0.30(0.32)	0.40(0.48)	0.20(0.22)	1.70(1.88)
iv	0.80(0.84)	0.32(0.30)	0.60(0.64)	0.68(0.78)	0.28(0.30)	2.68(2.86)
palp	0.38(0.38)	0.20(0.18)	0.22(0.20)	—	0.32(0.54)	1.12(1.30)

protuberances. The embolus lies on a membranous conductor retrolateral to the apophysis.

***Dardurus tamborinensis* n. sp.**
(Figs. 14-15, 19b)

MATERIAL EXAMINED

HOLOTYPE: Rain forest, Curtis Falls track, Mt Tamborine 50 km S. Brisbane, SE.Q. V. Davies, 22.vi.75, ♀, QM W4893.

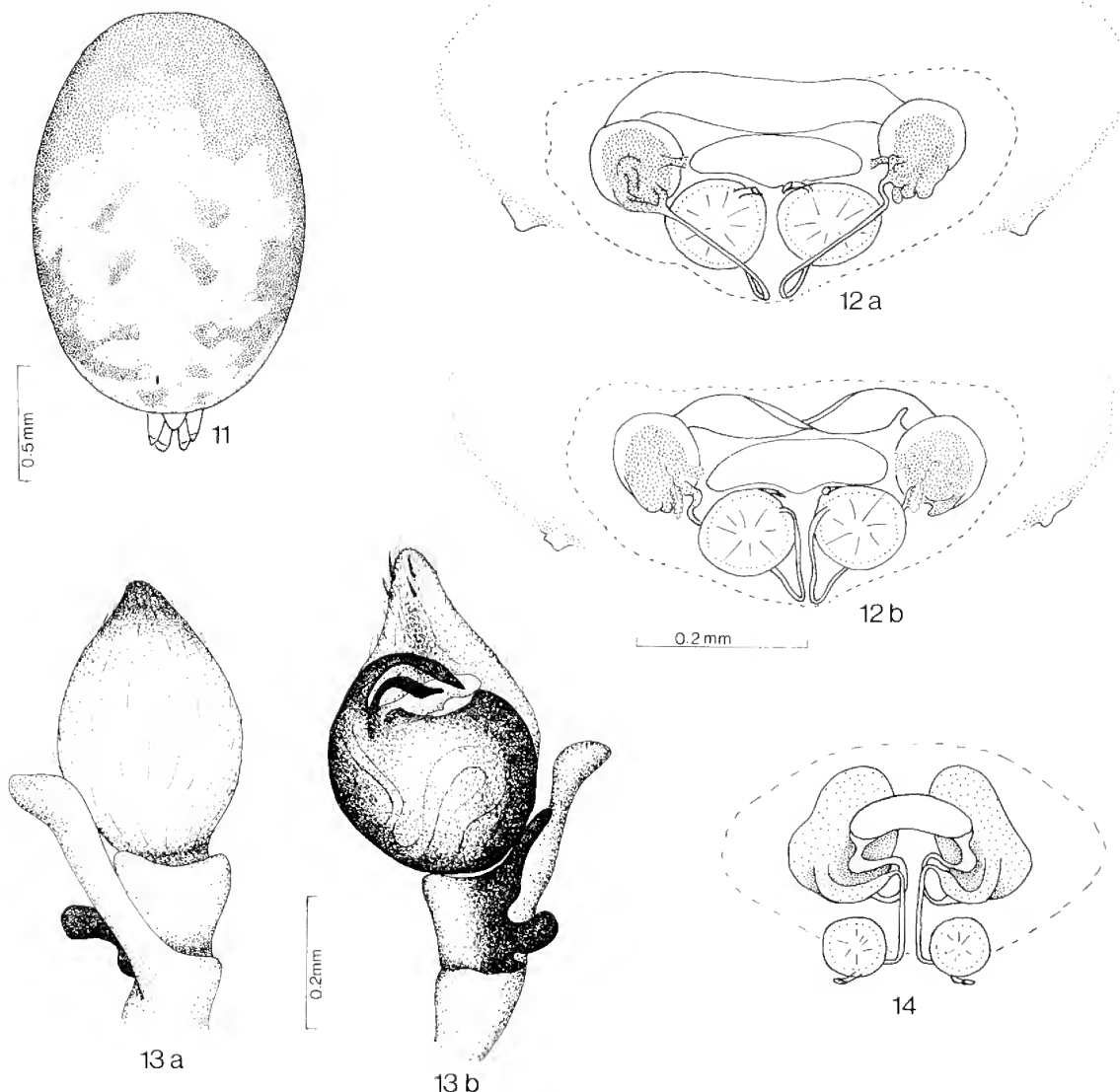
PARATYPES: Curtis Falls track, Mt Tamborine, SE.Q., V. Davies, 22.vi.75, 1♂, QM W4894; Curtis Falls track,

Mt Tamborine, SE.Q. V. Davies, C. L. Wilton, R. Raven, 10.vii.74, 2♂, 1♀, QM W4895.

DESCRIPTION OF FEMALE

CL 1.22; CW 0.84; AL 1.34; AW 0.90.

Cephalothorax and legs are pale yellow brown. Two small white 'thoracic patches' on each side of fovea present. Abdomen grey-black with lighter pattern. Eyes like *D. spinipes*. Five teeth on retromargin of chelicerae: 2 large and 2 small teeth of promargin. Labium wider than long 1:0.62. The sternum a little longer than broad 1:0.95.



FIGS. 11-12: *D. silvaticus*. 11, abdomen, dorsal; 12a, external epigynum, cleared; 12b, internal epigynum.

FIG. 13: *D. silvaticus*. 13a, palp, dorsal; 13b, palp, ventral.

FIG. 14: *D. tamborinensis*. External epigynum, cleared.

TABLE 3: LEG MEASUREMENTS OF *D. tamborinensis* ♀ AND (♂)

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
i	0.92(1.10)	0.38(0.40)	0.82(1.02)	0.68(0.92)	0.30(0.38)	3.10(3.82)
ii	0.72(0.88)	0.36(0.38)	0.58(0.72)	0.56(0.66)	0.26(0.32)	2.48(2.96)
iii	0.54(0.72)	0.30(0.30)	0.32(0.46)	0.44(0.62)	0.24(0.28)	1.84(2.38)
iv	0.88(1.04)	0.34(0.34)	0.66(0.84)	0.76(0.94)	0.32(0.38)	2.96(3.54)
palp	0.38(0.46)	0.20(0.14)	0.24(0.24)	—	0.36(0.56)	1.18(1.40)

Notation of Spines: Palp: tibia, p.2.1-2; tarsus, numerous small spines. First leg: femur, d.2.p.1. distal; tibia, v.2.p.0.1.1.1.1.(1).r.0.1.1.1.1; metatarsus, v.1.p.0.(1).1.1.1.r.0.1.1.1; tarsus, 0. Second leg: femur, d.2.v.1. distal; tibia, v.(1).2.p.0.1.1.1.1. r.0.1.0.1.1. metatarsus, v.1.p.0.1.1.1.1.1. r.0.1.0.1.0.1. Third leg: femur, d.1; patella, d.1.(1); tibia, d.0.(1).0.v.0.(1).2.p.0.1.1.r.0.1.(1); metatarsus, numerous small spines. Fourth leg: patella, d.1; tibia, d.1.0.0.(1).0.v.1.0.1.0.2.p.0.1.0.1.0. r.0.1.0.1.0; metatarsus, several spines. No calamistrum.

This species is ecribellate. The colulus was scanned and showed no spinning tubes. Anterior spinnerets are wider than the colulus. AS:colulus 1:0.70, unlike the other species described. The epigynal fossa is chitinised anteriorly (Figs. 14, 19b) and is about a third the width of the epigynum.

VARIATION: Cephalothorax length of ♀ QM W4895 is 1.30.

DESCRIPTION OF MALE

QM W4894: CL 1.34; CW 0.88; AL 1.24; AW 0.82.

Cephalothorax lengths varied from 1.16 to 1.40.

Colour and pattern are similar to ♀. 'Thoracic patches' absent. There are 5 teeth on retromargin of chelicerae.

Notation of spines: Prolateral distal spine on femur 1 is present as in ♀. This spine is also present in *D. silvaticus* but is absent in other ♂ *Dardurus* spp. examined. Apart from the presence of a dorsal spine on Femur IV the spination is like ♀.

Male palp: The embolus (Fig. 15b) arises anterior and prolateral to the apophysis in contrast to its position in the other species where it is

retrolateral. The apophysis here looks very like a 'median' apophysis. In view of the fact that *D. tamborinensis* is ecribellate it is assumed that the position of the embolus is secondary.

Dardurus nemoralis n. sp. (Figs. 16-18, 19d)

MATERIAL EXAMINED

HOLOTYPE: Wet sclerophyll forest, Cameron Falls track, Mt Tamborine, 50 km S. Brisbane, SE.Q., V. Davies, 22.vi.75, ♀, QM W4896.

PARATYPES: Cameron Falls track, Mt Tamborine, SE.Q. V. Davies, E. Howell, 22.vi.75, 2♀, 2♂, QM W4897.

DESCRIPTION OF FEMALE

CL 1.16; CW 0.74; AL 1.56; AW 1.00.

Cephalothorax and legs are a pale grey-brown. Small white 'thoracic patches' on each side of fovea are present. The abdomen is a dark grey-black with pale pattern posteriorly (Fig. 16). There are 4 teeth on retromargin of chelicera. The labium is wider than long 1:0.62. The sternum is longer than broad 1:0.89.

Notation of Spines: Palp: tibia, p.1.2; tarsus, numerous small spines. First leg: femur, d.1.p.1. distal; tibia, v.2.p.0.1.1.1.1.r.0.1.1.1.1; metatarsus, v.1.p.0.1.1.1.1.r.0.1.1.1; tarsus, 0. Second leg: femur, d.1.1.0; tibia, v.1.2.p.0.0.1.1.1.1.r.0.0.1.0.1.1; metatarsus, d.1.1.0.0.p.1.1.1.1.r.0.1.1.1. Third leg: tibia, d.0.1.0.v.1.0.1.p.1.1.0.r.1.1.0; metatarsus with numerous small spines. Fourth leg: tibia, v.1.0.1.1.p.0.1.0.0.r.0.1.0.0; metatarsus with several spines. Calamistrum 7 hairs proximal. AS:cribellum 1:1.10.

The epigynum (Fig. 17a, b) is very similar to *D. spinipes* but has weak lateral ridges. It is to be noted that in mounting the epigynum for drawing the sac-

TABLE 4: LEG MEASUREMENTS OF *D. nemoralis* ♀ AND (♂)

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
i	0.80(1.00)	0.36(0.44)	0.74(1.00)	0.62(0.84)	0.26(0.34)	2.78(3.62)
ii	0.70(0.78)	0.32(0.36)	0.50(0.64)	0.48(0.62)	0.24(0.28)	2.24(2.68)
iii	0.52(0.60)	0.28(0.30)	0.30(0.38)	0.38(0.54)	0.20(0.24)	1.68(2.06)
iv	0.78(0.90)	0.30(0.34)	0.54(0.74)	0.62(0.82)	0.26(0.32)	2.50(3.12)
palp	0.34(0.40)	0.18(0.18)	0.22(0.22)	—	0.30(0.58)	1.04(1.38)

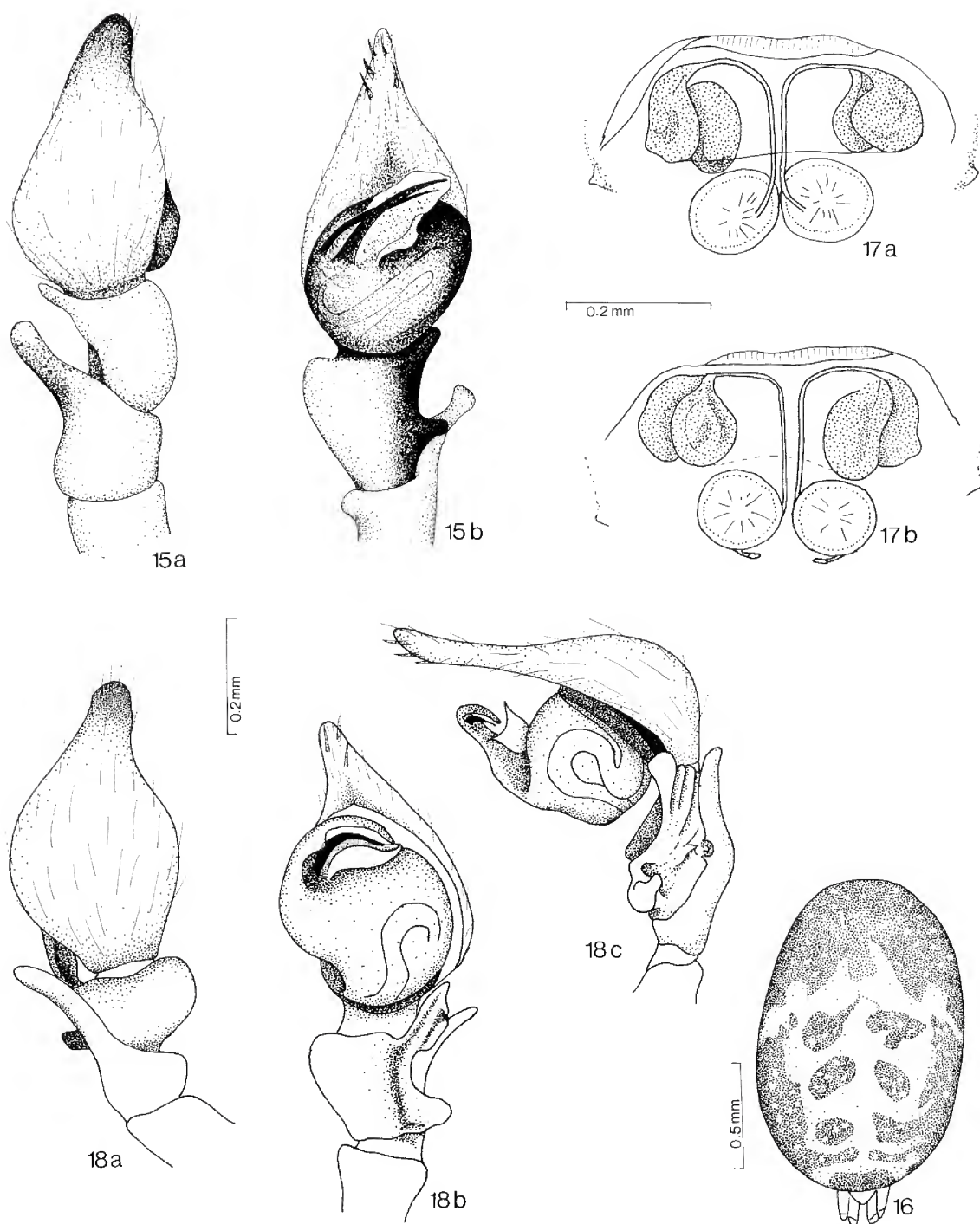


FIG. 15: ♂ *D. tamborinensis*. 15a, palp, dorsal; 15b, palp, ventral.

FIGS. 16–17: ♀ *D. nemoralis*. 16, abdomen, dorsal; 17a, external epigynum, cleared; 17b, internal epigynum.

FIG. 18: ♂ *D. nemoralis*. 18a, palp, dorsal; 18b, palp, ventral; 18c, palp, retrolateral.

like entrance ducts have been displaced (cf. Fig. 19d) so that the ducts to the spermathecae appear to rise anteriorly.

VARIATION: Cephalothorax lengths were 1.14–1.26.

DESCRIPTION OF MALE

QM W4897: CL 1.26; CW 0.88; AL 1.36; AW 0.88.

Cephalothorax length of the other ♂ 1.18.

Colour and pattern are similar to ♀.

Notation of spines in ♂ similar to ♀ except in following: First leg: femur, prolateral distal spine absent. Second leg: tibia, v.1.2.p.0.0.1.1.1.1.r.0.0.1.0.1.(1). Third leg: tibia, d.0.1.0.v.(1).0.1.p.1.1.0.r.1.0.0. Fourth leg: tibia, v.1.0.1.1–2.p.0.1.0.0.r.0.1.0.0.

Male palp: (Fig. 18a, b, c). The tibial apophysis lacks the median protuberances of *D. spinipes*. The embolus is retrolateral to the apophysis and rests on a membraneous conductor.

Dardurus saltuosus n. sp. (Figs. 19e, 20)

MATERIAL EXAMINED

HOLOTYPE: Yabba State Forest, Richmond Range, N. N.S.W., R. Raven, 28.ix.74, ♀, QM W4898.

PARATYPES: Yabba State Forest, Richmond Range, N. N.S.W., R. Raven, 28.ix.74, 1♂, 1 juv., QM W4899.

DESCRIPTION OF FEMALE

CL 1.36; CW 0.90; AL 1.60; AW 1.00.

Cephalothorax and legs light brown, abdomen grey-black with lighter pattern. 'Thoracic patches' at each side of fovea. Four teeth on retromargin of chelicerae. Labium wider than long 1:0.60. Sternum longer than wide 1:0.86.

Notation of spines: Palp: tibia, p.1–2.2; tarsus, numerous spines. First leg: femur, d.1.1.0.p.1 distal; tibia, v.2.p.0.1.1.1.1.(1).r.0.1.1.1.1; metatarsus, v.1.p.0.1.1.1.r.0.1.1.1; tarsus, 0. Second leg: femur, d.1.1.0; tibia, v.2.p.0.1.1.1.1.r.0.1.0.1.1; metatarsus, d.1.1.0.0.p.1.1.1.1.r.0.1.1.1; Third leg: tibia, d.0.v.1.0.1.p.0.1.1.r.0.0.1; metatarsus, numerous small spines. Fourth leg: femur, d.1.0.0; tibia,

v.1.1.1.1.p.0.1.0.(1).r.0.1.0.0; metatarsus, several spines. Calamistrum is well developed with 12 hairs. AS:cribellum 1:1.18.

The epigynum (Fig. 19e) has well developed lateral ridges and is twice as wide as long.

DESCRIPTION OF MALE

QM W4899: CL 1.36; CW 0.92; AL 1.33; AW 0.92.

Colour and pattern similar to ♀. 'Thoracic patches' absent.

Notation of spines: ♂ differs from ♀ in following spination. First leg: femur, d.1.0.0. Fourth leg: tibia, v.1.0.1.0.1.p.0.1.0.1.0.r.0.1.0.1.0.

Male palp: (Figs. 20a, b, c). The tibial apophysis has large anterior and posterior protuberances but no median ones. The embolus is retrolateral to the apophysis as in *D. spinipes*.

Dardurus agrestis n. sp. (Figs. 19f, 21)

MATERIAL EXAMINED

HOLOTYPE: Open grazed sclerophyll area, Black Duck Creek, near Junction View 90 km. W. Brisbane, SE.Q., V. Davies, 24.i.73, ♀, QM W4900.

PARATYPES: Black Duck Creek, SE.Q., V. Davies, 24.i.73, 1 penult. ♂, 2 juv., QM W4901.

DESCRIPTION OF FEMALE

CL 1.30; CW 0.88; AL 1.48; AW 1.00.

Cephalothorax and legs light brown, abdomen grey-black with lighter pattern. 'Thoracic patches' not visible. Four teeth on retromargin of chelicerae. Labium almost twice as wide as long 1:0.56. Sternum longer than wide 1:0.88.

Notation of spines: Palp: tibia, p.1.2; tarsus, numerous small spines. First leg: femur, p.1. distal; tibia, v.2.p.0.1.1.1.1.(1).r.0.1.1.1.1.(1); metatarsus, v.1.p.0.1.1.1.r.0.1.1.1.(1); tarsus, 0. Second leg: femur, d.1.0; tibia, v.2.p.0.1.1.1.1.r.0.1.0.1.0.1; metatarsus, d.1.1.0.0.p.1.1.1.1.r.0.1.1.1. Third leg: femur, d.1; tibia, d.0.1.0.v.1.0.1.p.1.1.0.r.0.1.1; metatarsus, numerous small spines. Fourth leg: tibia, d.0.p.0.0.1.0.r.0.0.0.1.0.v.1.1.1.0.2; metatarsus, several spines. Calamistrum absent. AS:cribellum 1:1.22.

TABLE 5: LEG MEASUREMENTS OF *D. saltuosus* ♀ AND (♂)

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
i	0.96(1.12)	0.42(0.46)	0.88(1.06)	0.76(0.94)	0.30(0.34)	3.32(3.92)
ii	0.74(0.86)	0.36(0.40)	0.60(0.70)	0.56(0.68)	0.26(0.26)	2.52(2.90)
iii	0.62(0.68)	0.32(0.26)	0.36(0.42)	0.50(0.60)	0.22(0.24)	2.02(2.20)
iv	0.90(1.00)	0.38(0.38)	0.68(0.80)	0.76(0.96)	0.32(0.36)	3.04(3.50)
palp	0.38(0.40)	0.24(0.20)	0.30(0.42)	—	0.40(0.70)	1.32(1.72)

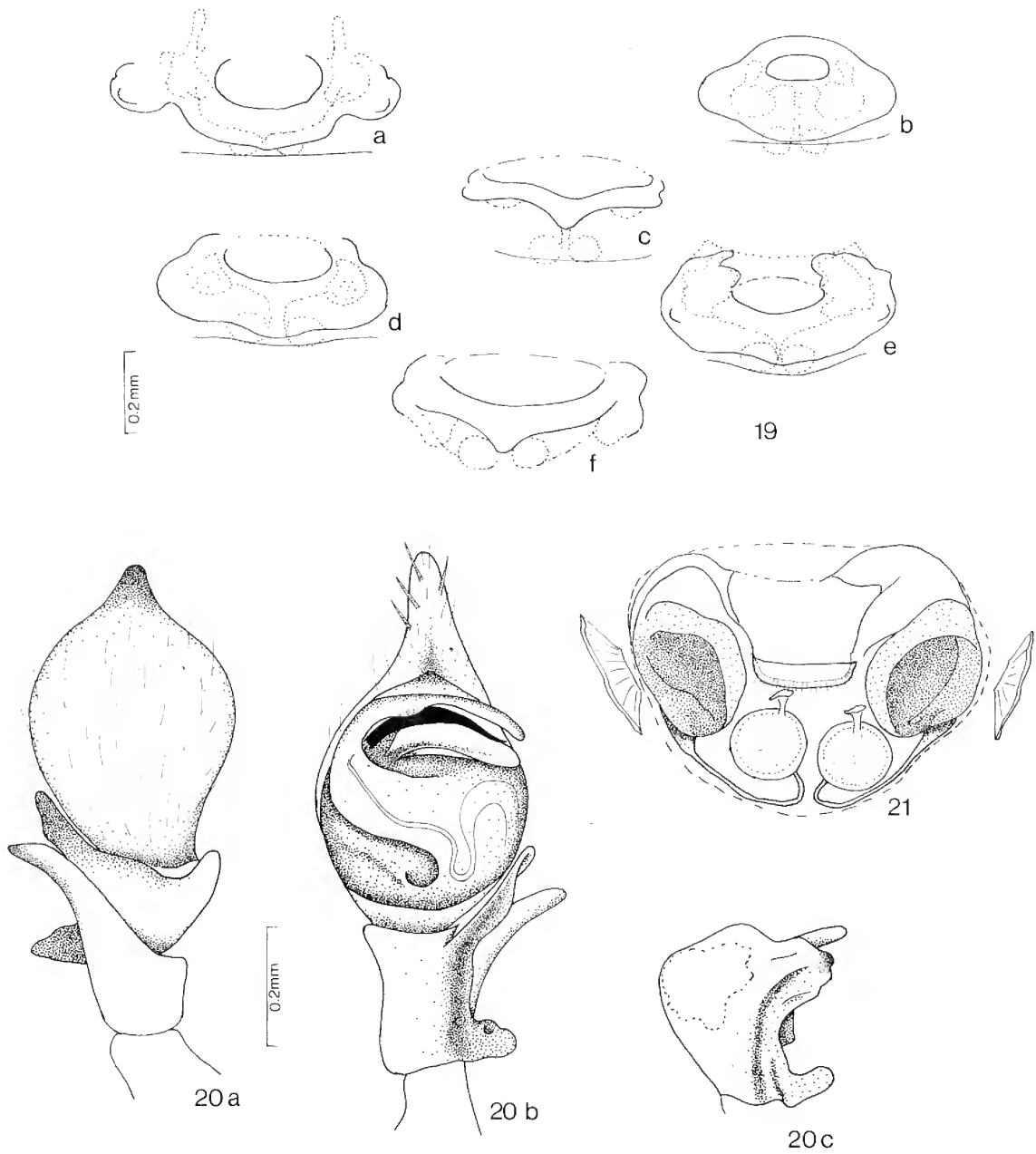


FIG. 19: External epigyna. 19a, *D. spinipes*; 19b, *D. tamborinensis*; 19c, *D. silvaticus*; 19d, *D. nemoralis*; 19e, *D. saltuosus*; 19f, *D. agrestis*.

FIG. 20: ♂ *D. saltuosus*. 20a, palp, dorsal; 20b, palp, ventral; 20c, tibia, with tarsal scar.

FIG. 21: ♀ *D. agrestis*. Internal epigynum.

TABLE 6: LEG MEASUREMENTS OF *D. agrestis* +

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
i	0.98	0.42	0.92	0.80	0.26	3.38
ii	0.80	0.36	0.64	0.64	0.24	2.68
iii	0.60	0.32	0.38	0.48	0.22	2.00
iv	0.90	0.34	0.72	0.78	0.32	3.06
palp	0.42	0.22	0.30	—	0.40	1.34

The epigynum (Fig. 19f, 21) has well marked lateral ridges.

VARIATION: A calamistrum of 7 hairs is present in the juveniles.

DESCRIPTION OF MALE

No adult ♂ has been collected. Measurements of a penultimate ♂ are: CL 1.20; CW 0.74; AL 1.42; AW 0.88.

KEY TO IDENTIFICATION OF *Dardurus* spp.

1. Four retromarginal teeth on chelicera; embolus retrolateral to apophysis; calamistrum usually present. 2
- Five retromarginal teeth on chelicera; embolus prolateral to apophysis; no calamistrum *D. tamborinensis*
- 2(1) Fossa of epigynum almost as wide as epigynum 3
- Fossa of epigynum not exceeding $\frac{1}{2}$ width of epigynum 4
- 3(2) Epigynum with marked lateral ridges *D. agrestis*
- Epigynum with weak lateral ridges *D. silvaticus*
- 4(2) Epigynum with marked lateral ridges 5
- Epigynum with weak lateral ridges *D. nemoralis*
- 5(4) External epigynum $2\frac{1}{2} \times$ wide as long; ♂ tibial apophysis with anterior, median and posterior protuberances *D. spinipes*
- External epigynum $2 \times$ wide as long; ♂ tibial apophysis with anterior and posterior protuberances. *D. saltuosus*

The decorated tubes of the different species are indistinguishable. The only similar tube seen is that of an undescribed sedentary clubionid which was found while looking for *Dardurus* in M.E. Queensland and NE. Queensland. It has a small flat silk disc with two openings and is found under logs in similar positions to *Dardurus*. At present the latter has a distribution limited to SE. Queensland and N. New South Wales.

Small pale 'thoracic patches' are present on the mature females of *D. spinipes*, *D. silvaticus*, *D. tamborinensis* (ecribellate), *D. nemoralis* and *D. saltuosus*. The : palpal tarsus seems unusually large in all the species. These characters, for which no explanation is offered, may be useful in placing *Dardurus* in a higher taxon.

CRIBELLUM AND COLULUS

The cribellum of *Dardurus* spp. provides a further example of the reduction and eventual loss of this spinning organ in the amaurobiids. *D. spinipes*, *D. silvaticus* and *D. tamborinensis* were examined with the scanning electron microscope for the presence of spinning tubes on the cribellum. *D. silvaticus* was found to have many more tubes than *D. spinipes* and there was none on the colulus of *D. tamborinensis*. There is further correlation in the reduction of the calamistrum from 9 hairs in *D. silvaticus* to 7 thin hairs in *D. spinipes* to the absence of a calamistrum in *D. tamborinensis*. Unlike the cribella of the other species, the colulus width of *D. tamborinensis* is narrower than that of the anterior lateral spinneret but it is still flat and semi-circular. The unsegmented structure of the spinning tubes is in contrast to the segmented tubes of cribella of other spiders examined. These included *Ixeuticus longinquus* (= *I. martius*) (Plate 60C, D) *Stiphidion facetum* (Plate 60E, F) *Paramatachia decorata* and several undescribed cribellates all of which are known to spin webs. The scanning micrographs show interesting differences in density of the tubes in *I. longinquus* and *S. facetum* which may be useful in separating the two groups. The reduction in number of spinning tubes in *Dardurus* spp. and their unsegmented nature as well as the absence of any web outside the tube suggest that the spinning function of the cribellum is reduced or even lost. It is certainly lost in *D. tamborinensis*. If the absence of web outside the tube of the sedentary *Dardurus* is associated with a decrease in dependence on the snare for capturing food, then perhaps this is compensated for by the development of the very long spines on the anterior legs. They are common features of many hunting spiders and are used in the capture of food.

POSITION IN THE AMAUROBIIDAE

Dardurus does not fit easily into any of the recognised subfamilies though it has affinities with Forster and Wilton's (1973) Amphinctidae notably in relation to the large chitinised epigynum with lateral ridges, the undivided fossa, and the presence of 'thoracic patches'. The undivided cribellum, the presence of a patellar apophysis, and perhaps the habit suggest Lehtinen's (1967) Matachiinae.

There are so many amaurobiid spiders yet to be described from Australia that it seems preferable to leave the decision of placement in the family until more are described.

ACKNOWLEDGMENTS

Special thanks are due to John Hardy of the Electron Microscope Centre, University of Queensland for his skill and enthusiasm. Thanks also to Sue Hiley for tracing and shading Figs. 3, 4, 7, 8, 10, 13 and 15.

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PLATE 59

A: *D. spinipes*. Camouflaged tube on under side of fallen log \times 3·6.

B: *D. silvaticus*. Scanning electron micrograph of cribellum and anterior lateral spinnerets \times 230.

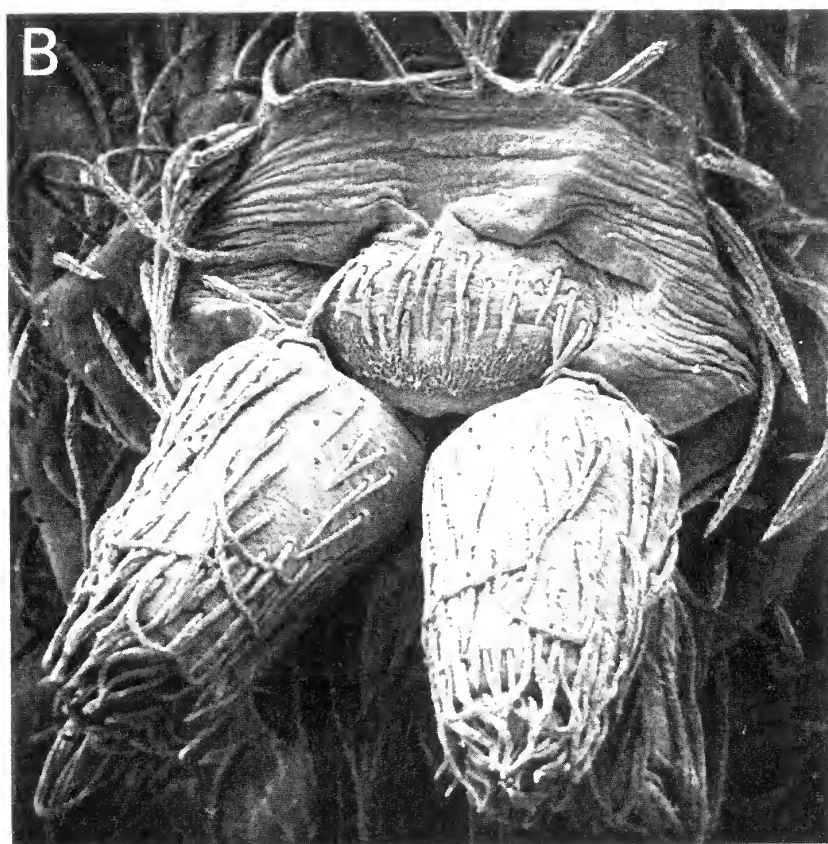
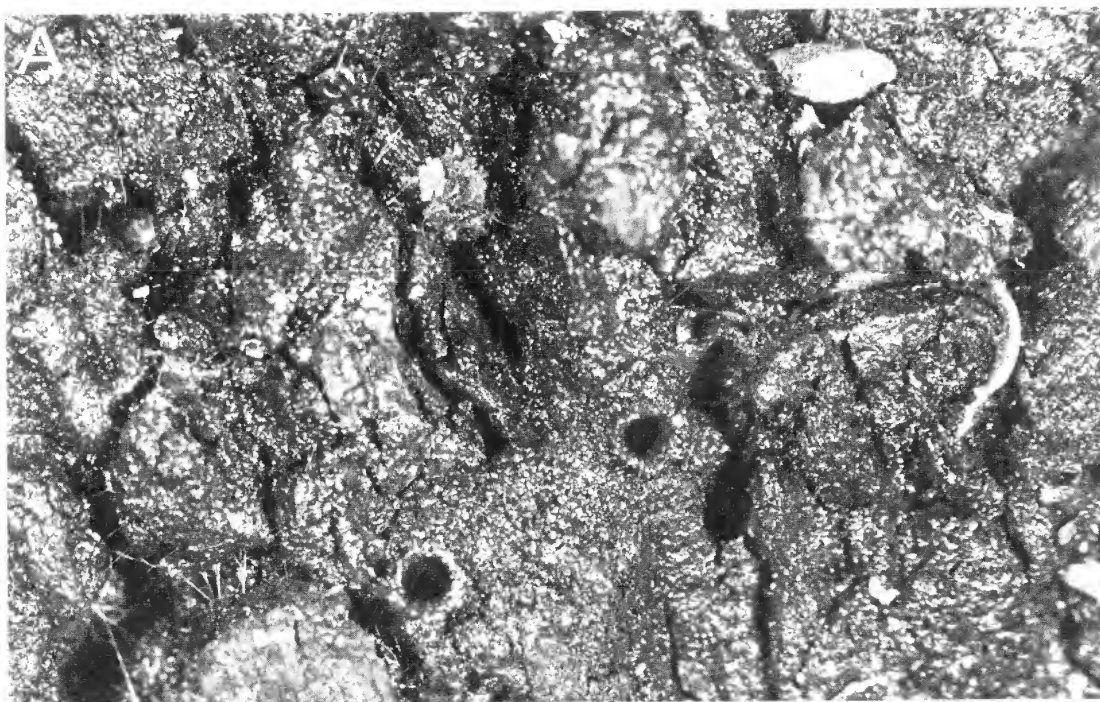
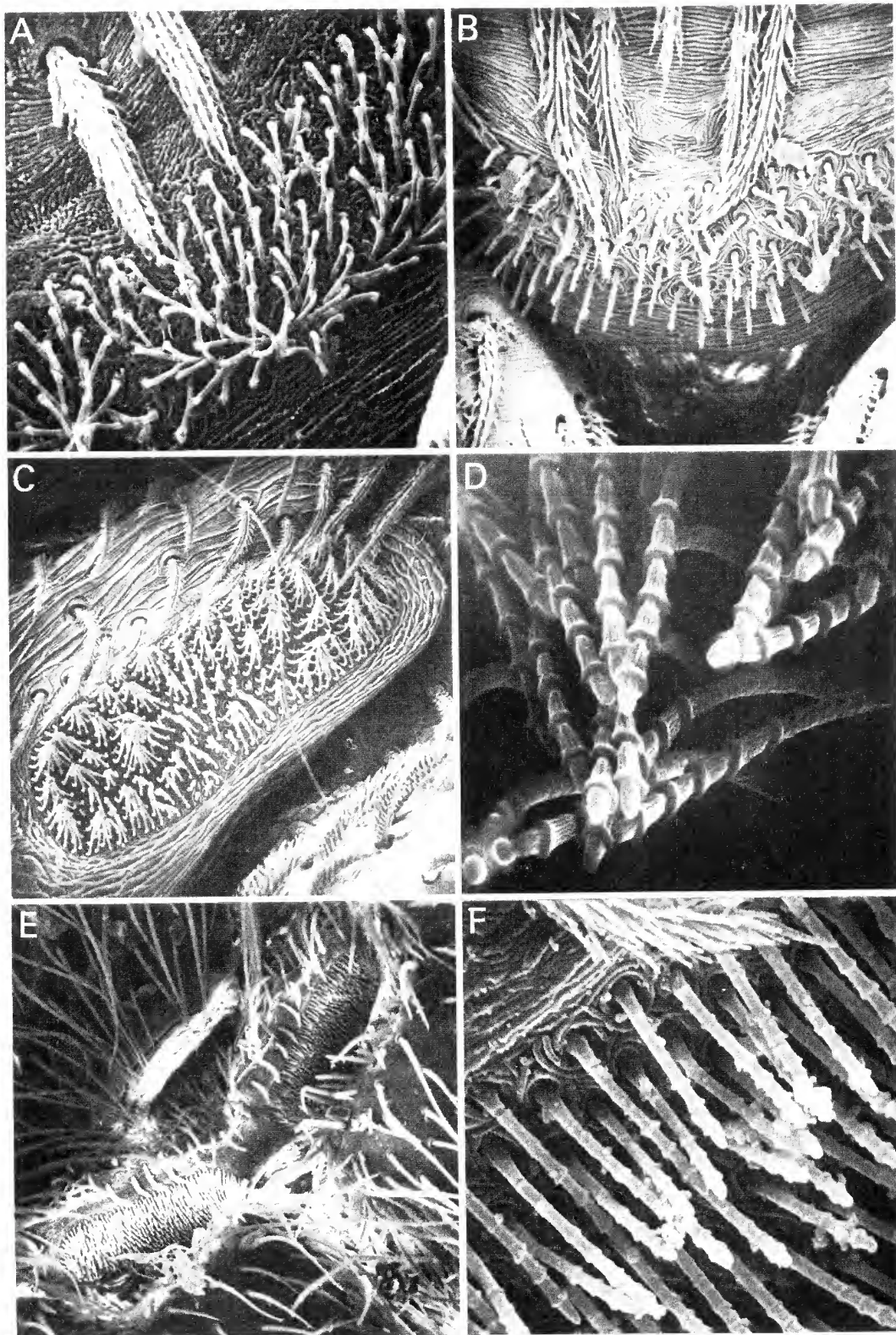


PLATE 60

Scanning electron micrographs A. : *D. sylvaticus*, spinning tubes on cribellum \times 1450; B. : *D. spinipes*, cribellum \times 1000, C. : *Ixeuticus longinquus*, half of divided cribellum \times 450; D. *I. longinquus*, spinning tubes of cribellum \times 6600; E. : *Stiphidion facetum*, cribellum \times 150; F. *S. facetum*, spinning tubes of cribellum \times 1800.





THE WOLF SPIDERS OF AUSTRALIA (ARANEAE: LYCOSIDAE): 7.
TWO NEW SPECIES FROM VICTORIA

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ABSTRACT

Two new species of Wolf Spider, *Lycosa mayama* and *Lycosa neboissi*, from near Melbourne, Victoria, are described.

An examination of the Wolf Spiders in the collection of the National Museum, Victoria (NM), kindly forwarded on loan by Mr A. Neboiss, disclosed the presence of two undescribed species in the suburban area of Melbourne. Because little systematic collecting of lycosids has been done in Victoria, the occurrence of new species near Melbourne is not unexpected.

Thirteen species of the subfamily Lycosinae have been recorded from Victoria (McKay 1973); New South Wales has over 40 species recorded, and Queensland has 32 plus a number of undescribed species. A considerable amount of collecting will be necessary to fully document the Australian Wolf Spiders and at this early stage, although some most interesting distribution patterns and speciation problems are emerging, such questions are premature with so much of the lycosid fauna unknown.

Lycosa mayama sp. nov.
(Fig. 1a-d)

MATERIAL EXAMINED

HOLOTYPE: National Museum, Victoria (NM), ♀ M (CL 8.3 mm), Werribee, Victoria, collector unknown, 22.ix.68. In spirit.

PARATYPES: Broadmeadows, Melbourne, Victoria, F. P. Spry, 27.ix.07, ♀ M (CL 6.5) : M (CL 6.8), NM.

DESCRIPTION (Based on the holotype.)

Carapace medium brown with a very faint longitudinal stripe commencing behind the PL eyes and continuing to the posterior margin; no lateral band visible; some darker radiating marks are barely visible; paturon and fang dark brown; labium, maxillae, sternum and coxae brown. Abdomen dark brown above and below; on the dorsal surface are numerous scattered light and dark

spots; ventral surface with a dark brown (possibly black in life) area from the epigastrie furrow to the base of the spinnerets, surrounded by scattered light spots within a dark rounded field (see Fig. 1a); sides streaked with light and dark brown flecks. Legs brown with diffuse dark brown to blackish blotches.

Anterior row of eyes very slightly procurved, AM larger than AL. Ratio of eyes AM:AL:PM:PL = 23:17:43:32; distance AM:AM 8, AM:AL 5, AM:PM 12, AL:PM 17, PM:PM 23. Clypeus to AM 24. Length of first eye row 100, length of second eye row 103 micrometer units. The distance between the AM and AL eyes to the PM eye was measured between the lens of the eyes.

Chelicerae with three promarginal teeth, the middle one largest; three retromarginal teeth, the two internal ones of about equal size, the exterior one much smaller and almost obsolete. Labium longer than wide.

Epigynum with a short median guide; the transverse guide narrow at the base of the median guide, broadening distally to almost truncate ends (Fig. 1b).

Femur of fourth leg with 1 + 1 + 1 dorsal spines.

VARIATION: The colour pattern of the holotype is partly faded due to preservation. The smaller paratypes lack the pattern on the ventral surface of the abdomen but in both specimens a faint longitudinal stripe is present on the carapace. One paratype has a brown longitudinal wedge-shaped median stripe on the anterior dorsal surface of the abdomen; this stripe is outlined in dark brown with a white spot on either side midway and a pair of more widely spaced white spots near the posterior tip.

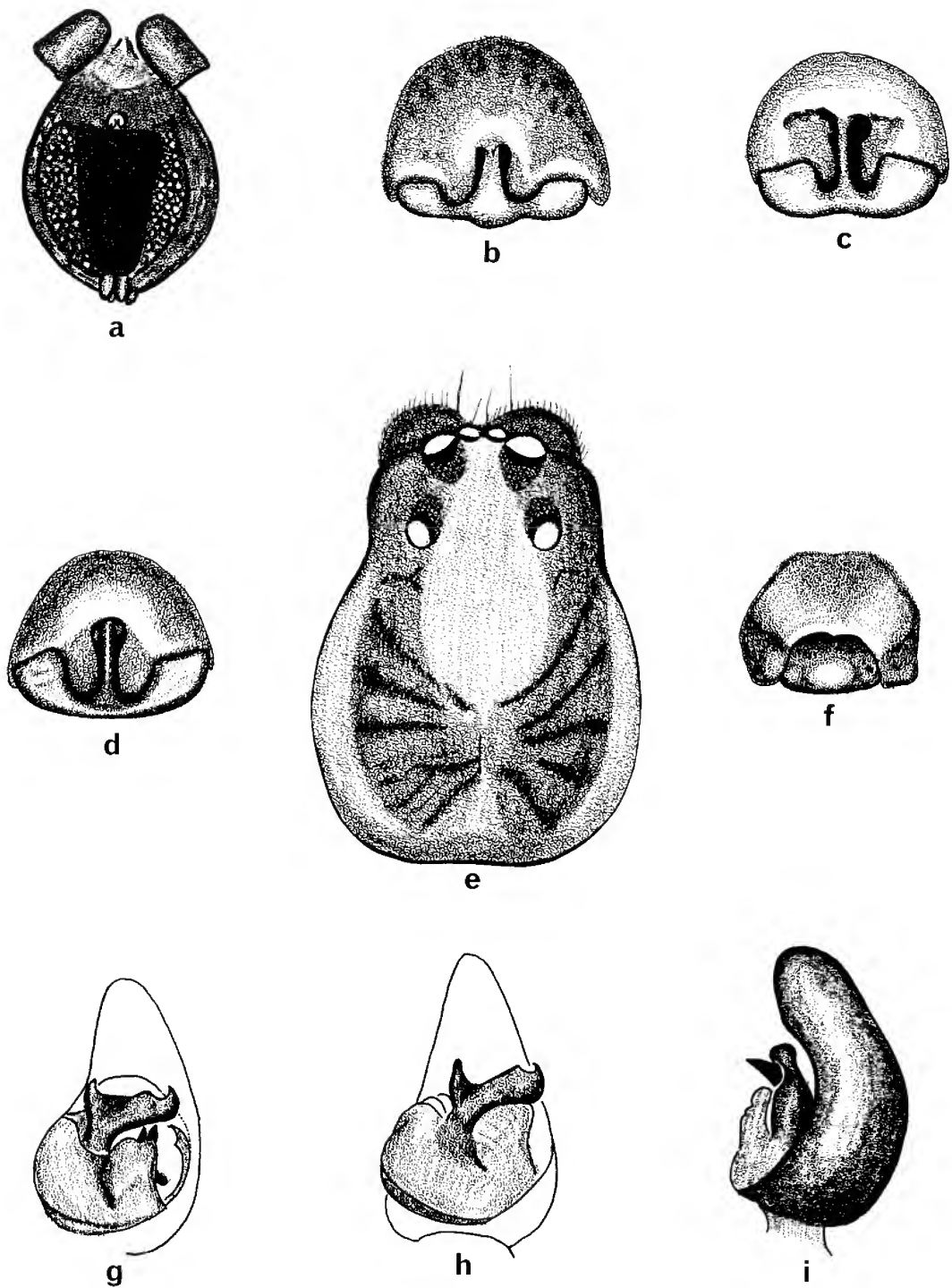


FIG. 1: a-d, *Lycosa mayama*: a, ventral surface of abdomen of holotype; b, epigynum of holotype; c-d, epigyna of paratypes.

e-i, *Lycosa nevoissi*. e, carapace of holotype; f, epigynum of holotype; g, palpal organ of paratype; h, palpal organ rotated slightly; i, palpal organ lateral view.

TABLE 1: MEASUREMENTS OF LEG SEGMENTS OF HOLOTYPE OF *L. mayama* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	5.4	2.9	4.1	3.6	2.3
2	4.8	2.8	3.4	3.4	2.4
3	4.6	2.3	2.9	3.6	2.3
4	6.4	2.8	4.7	5.7	2.7
Palp	3.0	1.5	1.6	—	2.3

The two paratypes have the ratio of eyes (expressed as per cent of the total width of the first row of eyes) AM:AL:PM:PL = 21:22:17:16; 41:45:35:37; distance AM:AM 9, 11; AM:AL 6, 8; AM:PM 17, 11; AL:PM 20, 16 (from lens of eye); PM:PM 26, 23. The clypeus equals the diameter of the AM. Length of the first eye row in micrometer units 85, 88; length of the second eye row in micrometer units 90, 93.

The epigyna of the holotype and the two paratypes are illustrated (Fig. 1b–d). Mature males were not collected.

DIAGNOSIS: A dark brown species; epigynum with a short narrow median guide, and a transverse guide that is narrow in the mid-section and has widely expanded truncate ends.

LIFE HISTORY

Unknown.

HABITAT

The two paratypes were collected from beneath stones.

DISTRIBUTION

Within 35 km of Melbourne, Victoria.

DERIVATION

From the aboriginal 'mayama' meaning stone.

Lycosa neboissi sp. nov.

(Fig. 1e–i)

MATERIAL EXAMINED

HOLOTYPE: National Museum, Victoria (NM), ♂M (C.L. 3.6 mm), Rosanna, northeast of Melbourne, Victoria, collected by A. Neboiss, 18 July 1954. In spirit.

PARATYPE: Rosanna, A. Neboiss, 5 June 1954, ♂M (C.L. 3.5 mm), NM.

DESCRIPTION

HOLOTYPE: Carapace light brown with a faint light median longitudinal stripe including a broad paler area behind the PL eyes, sides darker brown with radiating black-brown marks, and a pale lateral band (Fig. 1e); area around eyes black; paturon medium brown; labium, maxillae, sternum

and coxae uniform pale brown. Abdomen above pale brown to greyish with some scattered dark brown spots and blotches arranged in pairs along the median line, but somewhat distorted due to the wrinkled state of the abdomen; ventral surface and sides uniform grey brown. Legs pale brown; femora with dark blotches on the retrolateral surface and to a lesser extent the prolateral, dorsal and ventral surfaces; patellae with a conspicuous dark brown spot distally on either side; tibiae with three or four lateral blotches; remaining leg segments uniform pale brown or very faintly blotched.

Anterior row of eyes strongly procurved, the AL situated on a level below the AM; AM larger than AL; PM large, the distance between slightly greater than their diameter. Ratio of eyes AM:AL:PM:PL = 9:6:24:17; distance AM:AM 9, AM:AL 6, AM:PM 6, AL:PM 6, PM:PM 25. Clypeus to AM 14. Length of first eye row 46, length of second eye row 70 micrometer units.

Chelicerae with three promarginal teeth, the middle one largest; three retromarginal teeth of equal size. Labium longer than wide.

Epigynum rounded, the guide occupying all the epigynal depression (Fig. 1f).

Femur of fourth leg with 1 + 1 + 1 spines.

PARATYPE: Carapace similar to the female. Below carapace on the membrane above each coxa, are a pair of dark brown to black blotches, the posterior one of each pair being most conspicuous; the female has similar blotches above the coxae but these are not as well defined as in the male. Legs marked as in the female. Abdomen with a broad pale longitudinal median stripe, rounded anteriorly and gently tapering to touch the base of the spinnerets; sides darker with fine pale spots and numerous streaks and flecks of black-brown forming small black-brown blotches along the posterior margin of the pale longitudinal stripe; ventral surface with the dark pigmentation extending from the posterior sides to surround the spinnerets, and two widely spaced dusky bars commencing at the base of the lung-books and converging towards the middle of the ventral surface where they continue parallel to the base of the spinnerets.

TABLE 2: MEASUREMENTS OF LEG SEGMENTS OF HOLOTYPE OF *L. neboissi* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	2.5	1.3	2.0	1.8	1.0
2	2.3	1.3	1.7	1.9	1.1
3	2.0	1.2	1.5	2.0	0.9
4	2.8	1.2	2.4	3.1	0.9
Palp	1.2	0.6	0.8	—	1.0

Anterior row of eyes strongly procurved, the AM larger than the AL; PM larger than the distance between. Ratio of eyes AM:AL:PM:PL = 8:6:26:20; distance AM:AM 8, AM:AL 7, AM:PM 5, AL:PM 5, PM:PM 23. Clypeus to AM 9. Length of first eye row 44, length of second eye row 71 micrometer units.

Palpal organ with a well developed median apophysis which is narrow at the base but flaring out into a broad structure with a sharp blade-like cusp on the inner tip and a curved hook on the outer tip (Fig. 1g, h). The complete structure of the palpal organ was not studied.

DIAGNOSIS: A small species with a rounded epigynum having an expanded guide that fills the depression; male palpal organ complex (Fig. 1g, h, i); patellae with a conspicuous dark brown spot on each side, and dark marks on the membrane above the coxae.

LIFE HISTORY

Unknown.

HABITAT

Collected from garden in a recently developed suburb.

DISTRIBUTION

Suburban area of Melbourne, Victoria.

DERIVATION

Named after Mr A. Neboiss, National Museum, Victoria in appreciation of assistance given, and for collecting the type material of this new species.

ACKNOWLEDGMENTS

I record my appreciation of the assistance given to me by Mr A. Neboiss during my visit to the National Museum, Victoria, and his efforts to collect further specimens of *Lycosa nevoissi* for dissection.

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THE WOLF SPIDERS OF AUSTRALIA (ARANEAE: LYCOSIDAE): 8.
TWO NEW SPECIES INHABITING SALT LAKES OF WESTERN AUSTRALIA

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Queensland Museum

ABSTRACT

Two new species of Wolf Spider, *Lycosa alteripa* and *Lycosa salifodina*, are described from salt lake habitats in Western Australia.

Australia, due largely to position, size and topography is, with the exception of Antarctica, the driest of the continents; about 93 per cent of the land mass receives less than 510 mm, and 37 per cent receives less than 250 mm of rainfall per year. The driest area is located in South Australia, around Lake Eyre, where on the average less than 125 mm of rain falls annually. Evaporation in inland Australia is exceedingly high, and therefore permanent bodies of standing water—lakes, lagoons, and ponds—are rare. Much of the land surface is of low topography and is characterised by ephemeral rivers draining into salt lakes, and vast areas of uncoordinated drainage.

This area of internal drainage has innumerable playas, some saline, others gypsiferous or clayey. The small claypans and salinas are the sumps for local drainage and periodically fill with the runoff from surrounding areas which may be very extensive during cyclonic rains; the water evaporates leaving brine swamps or expanses of salt-encrusted clay, devoid of vegetation or surrounded by samphire (*Arthrocnemum*) communities with salt-bush and spinifex zones more distant. Some claypans have a continuous samphire margin, the inner part of which breaks up into clumps, and then on to vast clay flats that progressively become encrusted with evaporites until a layer of salt is formed. The largest salt lakes are frequently near or below sea level, and those of Lake Eyre and Lake Frome form a giant internal drainage basin some 1,250,000 km² in area. The evaporites are predominantly sodium chloride (90–95%) with lesser amounts of magnesium sulphate (5–7%) magnesium chloride (up to 4%) and calcium sulphate (up to 2.5%) (Johns and Ludbrook 1963), and originate from rocks which crop out in the

catchment area and, carried dominantly by shallow groundwater to a hot arid region of interior drainage, has then been concentrated at various times during the Quaternary (Wopfner and Twidale 1971, p. 138). The depth of the salt deposit varies from a thin encrustment to about 44 cm or more. Some playas or salinas are arranged in chains of white salt pans which may fill and have connected flow in periods of heavy rainfall, only to evaporate and redeposit the salt along the drainage system. The salt layer is therefore dissolved and reformed at irregular intervals, but may remain stable for many years during drought periods.

Figure 1 shows the extent of the uncoordinated drainage system in mainland Australia, and the major salt lake systems. The system is undoubtedly an ancient one and sufficiently stable to provide a suitable habitat for lycosid spiders. Hickman (1944) described *Pardosa eyrei* from the 'surface of North Lake Eyre two and a half miles from the shore' but no details were given concerning the burrow or life history. Immature *Lycosa* specimens have also been collected from lakes Callabonna, Ngapakaldia, and Palankarinna, in South Australia.

Two salt encrusted habitats were investigated in Western Australia; Lake Lefroy near Widgiemooltha, by Mr Athol Douglas of the Western Australian Museum, and a small claypan near the mouth of the Fitzgerald River by the author. The Wolf Spiders are readily captured using a head torch at night; the light is carried on the forehead, and by looking along the beam, the reflection of the light, appearing as pin points of pale emerald green, may be seen from spiders' eyes. On the surface of the salt lake the spiders are quite easily detected by this means, and individuals were

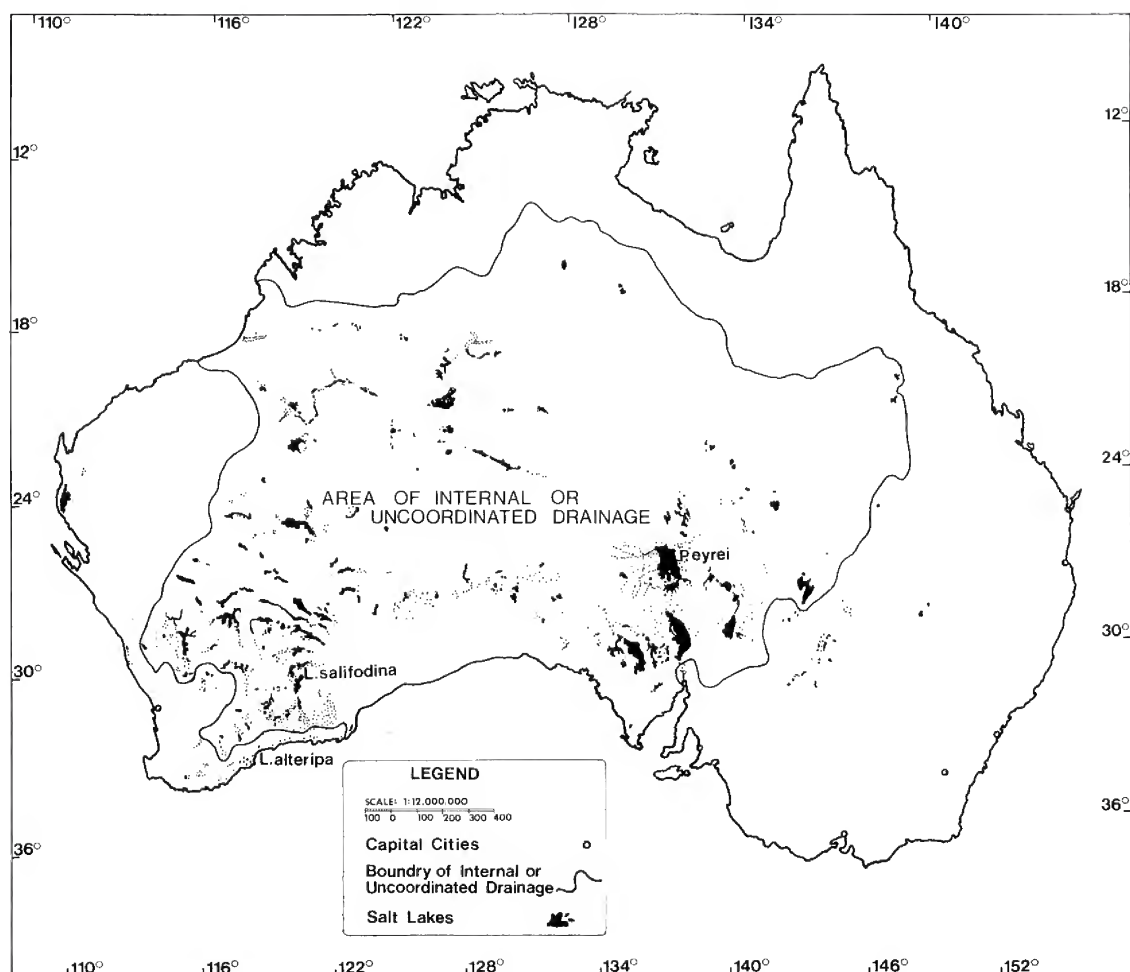


FIG. 1: Mainland Australia showing area of internal or uncoordinated drainage and distribution of salt lakes and claypans.

spotted a hundred yards out on the salt. Two quite unrelated species were discovered and are described below.

***Lycosa alteripa* sp. nov.**
(Fig. 2a-e)

MATERIAL EXAMINED

HOLOTYPE: Western Australian Museum WAM 71-40, ♂M (C.L. 9.6 mm), claypan near mouth of Fitzgerald River, W.A., collected by R. J. McKay and R. Prince, 11 July 1970. In spirit.

PARATYPES: Fitzgerald River (data as holotype), 1 ♀P 2 ♂M 2 ♀P 1J WAM 71-41-6. Claypan on road to Fitzgerald River—Susetta River junction, 13 July 1970, RJM, 1J WAM 71-47. Salt lake near Israelite Bay, W.A., 19 April 1974, A. V. Thomas, 1 ♀M WAM 74-501.

DESCRIPTION (Based on the holotype.)

Carapace pale grey to smoke white; radiating narrow wedges of charcoal grey originate near the white foveal area, almost reach the lateral margin, and have a pearl grey to white spot immediately behind or at their extremity; face silver grey; paturon smoke grey, fang black; labium and maxillae pale brown, sternum dark brown covered with grey hair; coxae pale grey-brown. Abdomen smoke grey above and below, an ornate pattern of charcoal grey is present on the dorsal surface (Fig. 2a), sides and venter uniform pale smoke grey. Legs pale grey-brown to pinkish grey with white hair and conspicuous dark brown spines; femora with two slightly darker brown blotches above, sides

and ventral surface pale; patellae with the proximal half mid-brown on the dorsal surface, pale below; tibiae of the first pair of legs dark charcoal brown, remaining leg segments dark brown; tibiae of the third and fourth legs with a basal dark half-band, a mid half-band of brown, and the extremity dark tipped; remaining leg segments pale brown; palp pale smoke grey, cymbium darker grey.

Anterior row of eyes procurved, AM larger than AL. Ratio of eyes AM:AL:PM:PL = 16:14:35:27; distance AM:AM 7, AM:AL 5, AM:PM 6, AL:PM 7, PM:PM 23. Clypeus to AM 10. Length of first eye row 75, length of second eye row 89 micrometer units.

Chelicerae with 3 promarginal teeth on the right side, the middle one largest; 4 promarginal teeth on the left side, the second one largest; three retro-marginal teeth of about equal size on both sides. Labium longer than wide.

The palpal organ differs from all the known Australian *Lycosa* species in having the secondary conductor sclerotised (Fig. 2b, d). The median apophysis has a recurved hook-like tip. A dissection of the male palp was not made, and therefore the structure remains to be studied in full when additional specimens are collected.

VARIATION: Males, females and juveniles are similarly patterned, the very small examples being somewhat more dark grey. Some specimens have the light background colour almost pure white with a grey-green pattern dorsally, occasionally tinged with mauve or pink. The undersurface of the abdomen is white without a pattern in males, but may be tinged with yellow in mature females.

The eye diameters and interspaces of the holotype and paratypes are given as a per cent of the total width of the first row of eyes, in Table 2; all specimens have the first row of eyes shorter than the second row.

The male palpal organ is illustrated in Fig. 2b, d; the epigynum of the female in Fig. 2c, and the internal genitalia of the female in Fig. 2e.

SIZE RANGE: Mature female 11.1 mm; Mature males 9.0 to 9.6 mm.

TABLE 1: MEASUREMENTS OF LEG SEGMENTS OF HOLOTYPE OF *L. alteripa* IN MM

Leg	Femur	Patella	Tibia	Metarsus	Tarsus
1	7.7	3.3	5.6	8.7	3.7
2	7.6	3.3	5.5	9.2	3.7
3	7.2	3.2	4.6	9.4	3.8
4	9.0	3.2	6.3	11.3	4.4
Palp	4.0	1.8	2.0	—	—

DIAGNOSIS: The mature female epigynum has a short median guide with a recurved transverse guide (Fig. 2c). The male palpal organ has a sclerotised secondary conductor with a hook-like median apophysis. All specimens are pale grey to smoke-white without a ventral pattern on the abdomen.

LIFE HISTORY

Unknown.

HABITAT

Claypans of southeastern Western Australia. All specimens were collected more than 2 to 3 metres from the margin of the claypan where the dried grey clay was encrusted with salt crystals. The mature males were found widely scattered over the middle of the dry claypan and none were seen near the samphire covered margins of the claypan where a rather robust brown *Lycosa* species (?*L. egena*) was very common.

BURROW

One juvenile was collected from a shallow open burrow near the middle of the claypan but as no other burrows were located it is possible that the burrows of mature specimens are closed with a tightly fitting door or lid.

DISTRIBUTION

Southeastern Western Australia, but possibly widespread on Western Australian inland and dry coastal claypans and saltpans.

DERIVATION

From the aboriginal 'alteripa' meaning claypan.

TABLE 2: EYE DIAMETERS AND INTERSPACES OF *Lycosa alteripa* CONVERTED TO PER CENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd. No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
Holotype	♂M	9.6	21	19	47	36	9	7	31	8	9
WAM74-501	♀M	11.1	20	15	45	40	10	10	34	11	11
WAM71-41	♂M	9.4	21	18	47	41	8	8	33	11	8
WAM71-42	♂M	9.0	20	17	47	44	10	9	36	9	9

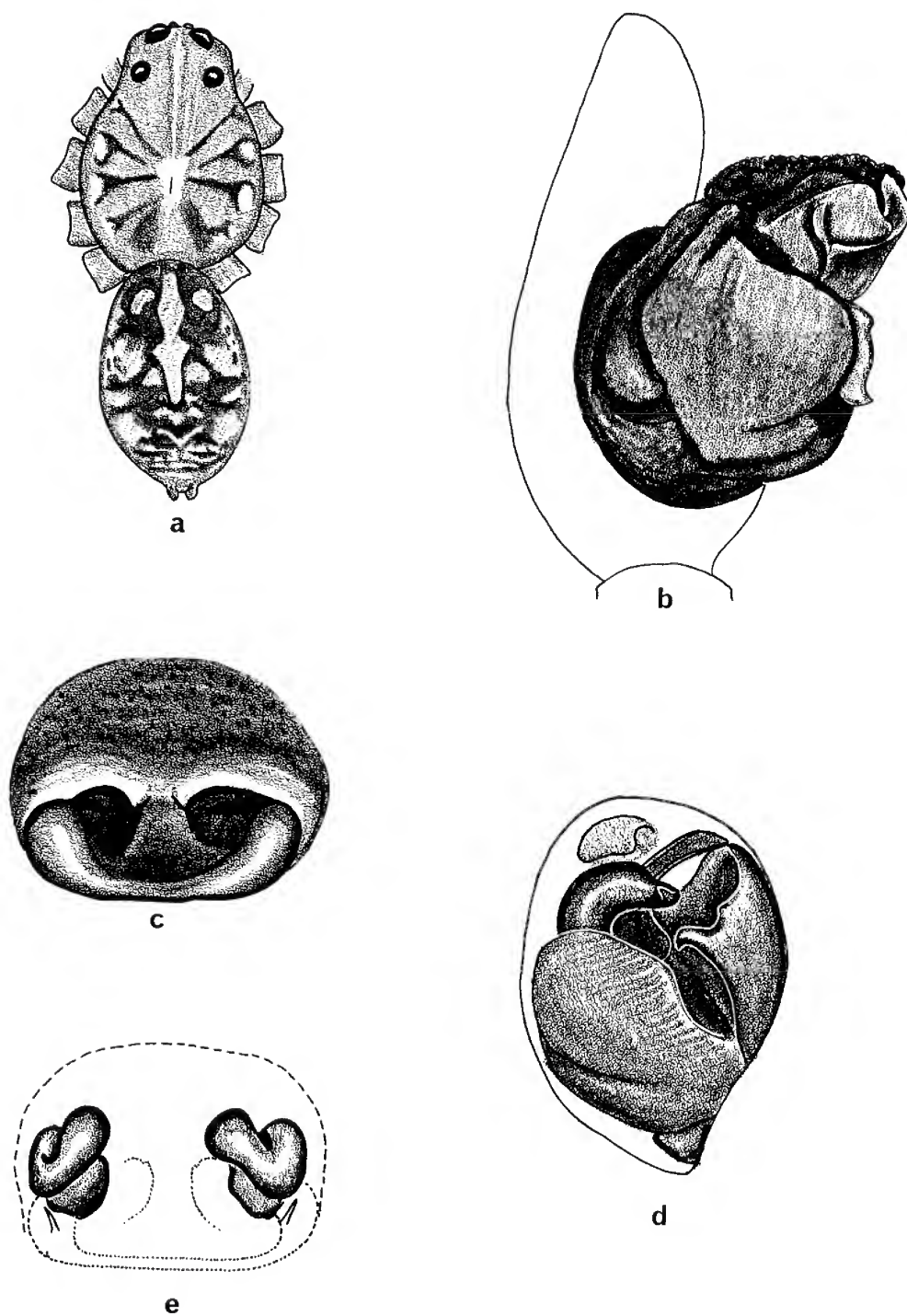


FIG. 2: *Lycosa alteripa*. a, holotype; b, male palpal organ of WAM 71-41 slightly expanded; c, epigynum of WAM 71-501; d, male palpal organ of WAM 71-41; e, internal genitalia of WAM 71-501.

***Lycosa salifodina* sp. nov.**
(Fig. 3a-g)

MATERIAL EXAMINED

HOLOTYPE: Western Australian Museum WAM 69-369, ♀M (C.L. 14.1 mm), Lake Lefroy, Widgiemooltha, W.A., collected by A. M. Douglas and L. Koch, 24 January 1968. In spirit.

PARATYPES: Lake Lefroy, Widgiemooltha, W.A., 24 January 1968, A. M. Douglas, L. E. Koch, ♀M WAM 69-104, 3♀M WAM 69-366-8, 3♂M 2♂M 22J WAM 69-370-94; March 1970, A. M. Douglas, 4P WAM 70-56-9, ♀M WAM 71-1747; 11.iv.1971, A. M. Douglas, 1♀M 1J QM W4543.

DESCRIPTION (Based on the holotype.)

Carapace brown, covered with pink-tinged white hair; where the hair has been rubbed off some faint brown radial lines may be discerned, but these are not present in life; face white with a pink tinge; paturon white with the lower part black; labium and maxillae black; sternum and ventral surface of coxae black. Abdomen with the dorsal surface pink-white; a brownish longitudinal stripe reaching half length of abdomen with two white spots on each side at the middle; two pale-brown chevron-shaped transverse bars posteriorly; ventral surface pink to white with two dark brown to black-brown longitudinal stripes tapering posteriorly and fading before the spinnerets, the area between the two stripes is brownish-pink in life becoming very pale brown after preservation (Fig. 3a); area anterior to epigastric furrow and over lung-book covers brown, becoming dark brown after preservation. Legs pink to ash-grey, spines black; extremities of

VARIATION: Males and females are similarly coloured; juveniles lack the pattern on the ventral surface of the abdomen, and in mature specimens this pattern may consist of two dark-brown to black converging broad stripes or lines, sometimes with a faint dusky line or black bar between, or occasionally the area between the two or three bars is pigmented with grey, brown, or black to the extent that the pattern appears as a dark brown somewhat rectangular blotch with the lateral margins darker. Some specimens have the ventral tips of the tibiae dark brown, grey or black distally; in large males the anterior pairs of legs may have the tibiae, metatarsi and tarsi dark brown, greyish or almost black-brown with a greyish tinge. In life the spiders may be white, off-white or pink-white in colour.

Juveniles have very prominent PM and PL eyes. The eye diameters and interspaces of the holotype and six paratypes are recorded as a per cent of the total width of the first row of eyes in Table 4.

Little variation was found in the shape of the epigynum, that of the holotype and a paratype is the femora, tibiae and metatarsi with a dark brown to black edge; undersurface of metatarsi and tarsi brown, the anterior pair of legs with the distal half of the tibiae, the whole of the metatarsi and tarsi black below, becoming dark brown after preservation.

Anterior row of eyes procurved, AM larger than AL, PM eyes large and conspicuous measuring about 2 mm in diameter. Ratio of eyes AM:AL:PM:PL = 11:7:31:29; distance AM:AM 7, AM:AL 4, AM:PM 5.5, AL:PM 4, PM:PM 23. Clypeus to AM 7. Length of first eye row 51, length of second eye row 79 micrometer units.

Chelicerae with three promarginal teeth, the middle one largest; three retromarginal teeth of about equal size. Labium longer than wide.

Epigynum elongate with a well developed median guide somewhat expanded anteriorly and terminating in a moderately broad transverse guide (Fig. 3c).

TABLE 3: MEASUREMENTS OF LEG SEGMENTS OF HOLOTYPE OF *L. salifodina* IN MM

Leg	Femur	Patella	Tibia	Metatarsus	Tarsus
1	10.3	5.3	7.5	8.7	3.5
2	9.7	5.0	7.5	9.0	3.5
3	9.8	4.5	6.5	8.8	3.9
4	11.2	4.8	7.9	11.6	4.1
Palp	5.2	2.5	3.2	—	3.3

TABLE 4: EYE DIAMETERS AND INTERSPACES OF *Lycosa salifodina* CONVERTED TO PER CENT OF THE TOTAL WIDTH OF THE FIRST ROW OF EYES

Regd No.	Sex	C.L.	AM	AL	PM	PL	AM:AM	AM:AL	PM:PM	AM:PM	AL:PM
Holotype	♀M	14.1	22	14	61	57	14	8	45	11	8
WAM69-104	♀M	13.8	22	14	62	56	12	10	46	11	11
WAM69-366	♀M	12.2	22	15	60	57	14	7	44	11	10
WAM69-367	♀M	13.2	22	14	63	53	13	12	44	11	8
WAM69-368	♀M	12.9	22	15	64	60	11	9	45	9	6
WAM69-370	♀M	13.2	23	12	63	51	10	12	43	10	8
WAM69-371	♂M	12.3	23	15	67	49	9	9	40	12	10

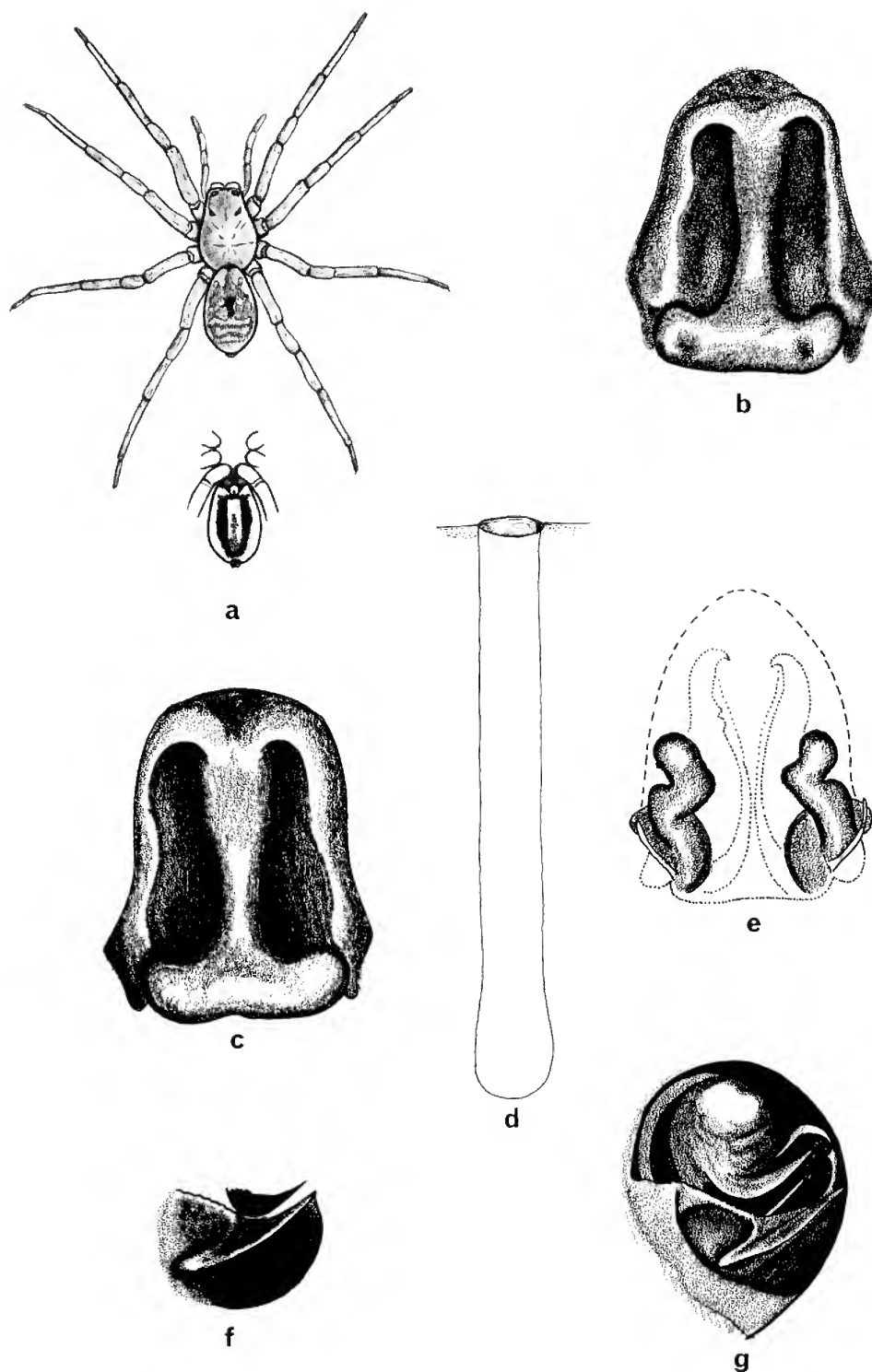


FIG. 3: *Lycosa salifodina*. a, holotype showing ventral surface of abdomen; b, epigynum of WAM 69-104; c, epigynum of holotype; d, burrow construction; e, internal genitalia of WAM 69-104; f, median apophysis and embolic guide of WAM 69-371; g, male palpal organ of WAM 69-371.

illustrated in Fig. 3c, b. The internal genitalia of one paratype female is shown in Fig. 3e. The male palpal organ has a blade-like median apophysis (Fig. 3f) and a curved pointed embolic guide (Fig. 3g). The structure of the palpal organ resembles that of some members of the bicolor group (McKay 1973) and is a fairly common basic type found in many of the larger *Lycosa* species.

SIZE RANGE: Mature females C.L. 12.1 to 13.8 mm. Mature males C.L. 11.8 to 12.3 mm.

DIAGNOSIS: A large species that inhabits salt-pans; the epigynum is elongate (Fig. 3c); the eyes are highly developed and quite prominent; the ventral surface of the abdomen has two converging dark brown bars in most mature specimens.

LIFE HISTORY

Mature males and females are present throughout the summer months; juveniles are common in April.

HABITAT

All specimens were collected from the open salt surface of Lake Lefroy, many being scattered all over the salt lake and only a few specimens near the periphery.

BURROW

Mr A. Douglas recorded the burrows as being open, vertical, and some 15 cm (5 to 6 inches) deep into the salt (Fig. 3d). The spiders were found to be 'sitting out in the middle of the lake perched directly over the burrow entrance'. Nothing is known about their behaviour, feeding habits, physiology, or how the spiders survive during rain or flood conditions.

DISTRIBUTION

Lake Lefroy, Widgiemooltha, Western Australia.

DERIVATION

From the latin meaning 'salt-mine'.

DISCUSSION

The salt lakes can be considered as 'island' habitats with infrequent or no contact with each other. These 'islands' vary in size from a few hectares to many km², and may be completely isolated or joined by dried watercourses or ribbons of salt encrusted clay deposits to form chains of lakes (Fig. 1). Such 'island' habitats provide valuable opportunities for studying the speciation of the salt lake Wolf Spiders, and are ideal for constructing models for the study of population dynamics.

Nothing is known of the biology of the salt lake species. The physiology of an animal that occupies a burrow constructed in salt, and is subject to extreme dessication, occasional floods, and high temperatures, is worthy of investigation. Much additional collecting is necessary to record the lycosid species on the salt lakes, and their distribution.

ACKNOWLEDGMENT

I gratefully acknowledge the assistance of Mr Athol M. Douglas of the Western Australian Museum, in collecting specimens of *Lycosa salifodina* and describing the burrow.

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THE MACROBENTHOS OF BRAMBLE BAY, MORETON BAY, QUEENSLAND

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ABSTRACT

As part of a study of the possible effects of enlarging Brisbane Airport upon the biota of adjacent areas, the macro-benthos of Bramble Bay was investigated. Sites at c. 1 km apart were sampled in duplicate with an 0.1 m² van Veen grab and sieved through 1 mm mesh. The data gave two three-dimensional matrices; of ca 190 spp \times 27 sites \times 7 seasons (at three month intervals) and of ca 190 spp \times 48 sites \times 2 years respectively.

The number of species is roughly half that from a current survey of Middle Banks and roughly half that from a past study near Peel Island, both in Moreton Bay.

Analysis of the 3D matrices followed different patterns from those of Stephenson, Williams and Cook (1974), and these are detailed. They involved transformations using $\log(n + 1)$; also the species were standardized by totals prior to species classification. Data were scanned for outstandingly large values, and interactions of sites and times were explored via times classifications within site-groups.

Site classifications gave topographically coherent groups which generally followed an onshore-offshore sequence. The onshore sites, those most likely to be effected by airport construction, are characterized by *Spisula* and *Xenophthalmus* and have the highest populations but the lowest Shannon diversities of those investigated. The 48 sites data showed a site-group in proximity to the outflow of the Brisbane River.

Season classifications showed scarcely any grouping of similar seasons from two different years but instead groups of species persisted for c. 6-9 months and were then replaced by other groups. These temporal changes may be related to variations in runoff from land drainage and are most obvious in the area closest to the Brisbane River outflow.

Changes with time occur in almost all species. The magnitude of the time-changes suggests that 'base-line' studies for environmental impact statements in comparable situations (shallow water with some river influence) should involve extensive chronological replication. Prediction of the effects of airport construction would have been hazardous on the basis of present data because of other human activities in the area. A catastrophic flood ended the present study, caused unpredicted changes in the biota, and its effects will be described in a later paper.

This investigation was sponsored by the Australian Department of Housing and Construction and by the Queensland Department of the Coordinator General, and is part of a study of the possible effects of reclamation of an area east of the present Brisbane Airport. This would destroy mangroves, partly fill certain tidal creeks, and alter drainage patterns into the study area. It was hoped that a 'before' study of the macrobenthos of the area would lead to predictions of 'after' effects.

A relatively small area of Bramble Bay was sampled for macrobenthos at three-month in-

tervals and a larger area was sampled on successive Septembers. Experience gained at Peel Island in Moreton Bay by Stephenson, Williams and Cook (1974) suggested that a prolonged investigation might be required and the present work was planned to extend for an initial two years. An extreme flood in January 1974 caused dramatic changes in the biota and these will be considered in a later paper.

The data form two separate three dimensional groups: I of c. 190 species \times 27 sites \times 7 seasons, and II of c. 190 species \times 48 sites \times 2 years. To

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analyse data of this complexity requires numerical methods; present methods follow immediately upon the techniques of Williams and Stephenson (1973) and Stephenson, Williams and Cook (1974). They also follow up on the M.Sc. thesis of Raphael (1974) which dealt with seasonal data to March 1973 and this should be consulted for many relevant details e.g. sediment analyses, winds, rainfall. The present study involves three more seasons and more derivations from the data, and modifies certain aspects of the methods and conclusions.

SAMPLING AREA AND SAMPLING DETAILS

Moreton Bay has been described by Stephenson, Williams and Lance (1970), Maxwell (1970) and Newell (1971). The relevant portion is shown in Fig. 1 and the study area in Fig. 2.

Difficulties were encountered in selecting sampling sites and sampling times. Results obtained by Stephenson, Williams and Cook (1974) suggested that for one area of Moreton Bay it would have been desirable to have intersite distances of c. 0.25 km, to obtain quintuplicate catches of 0.1 m² at

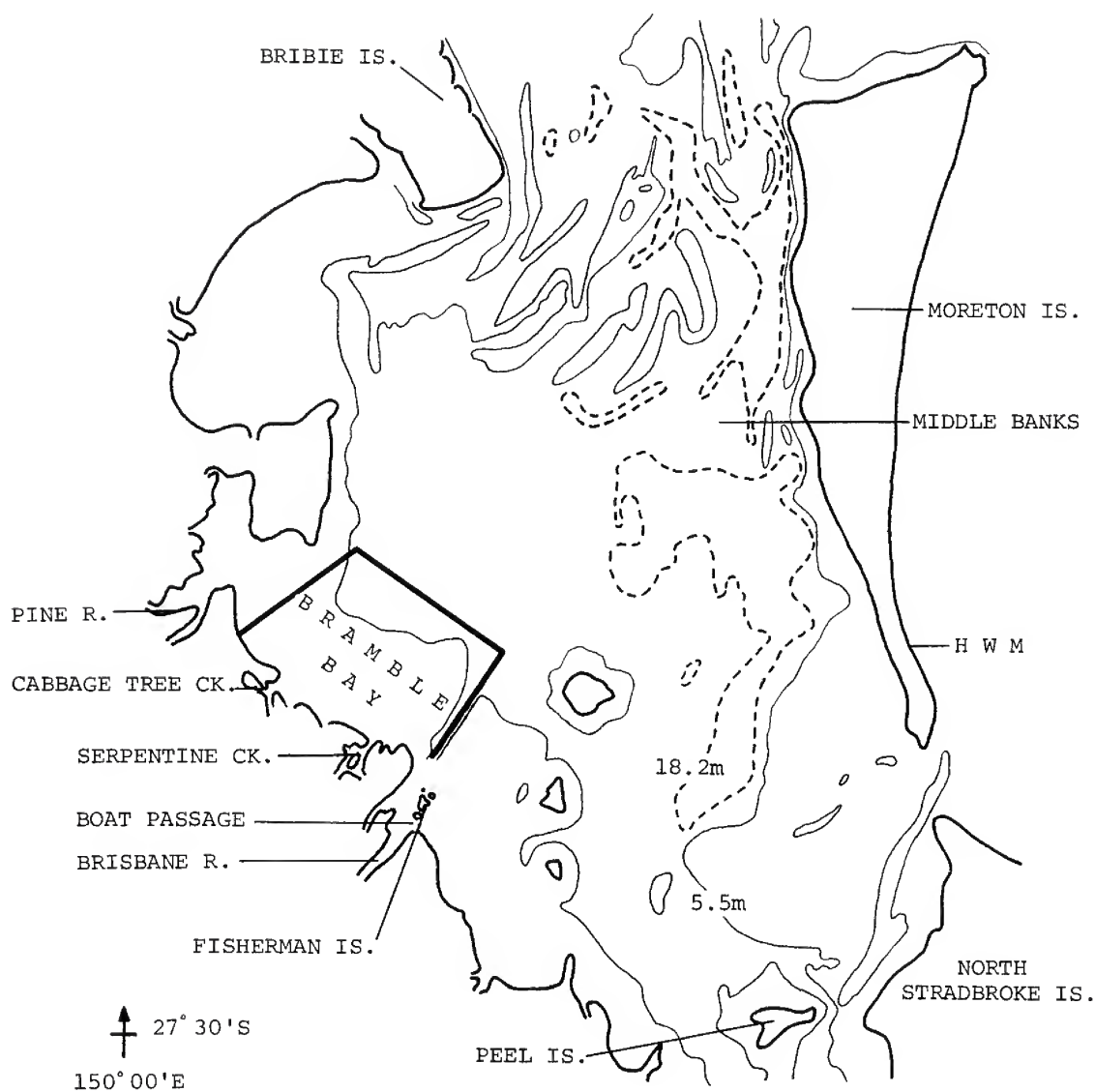


FIG. 1: Moreton Bay showing localities mentioned in text. Thick line high water mark, thin line 5.5 m (3 fm), broken line 18.2 m (10 fm). Very heavy line encloses sampling area.

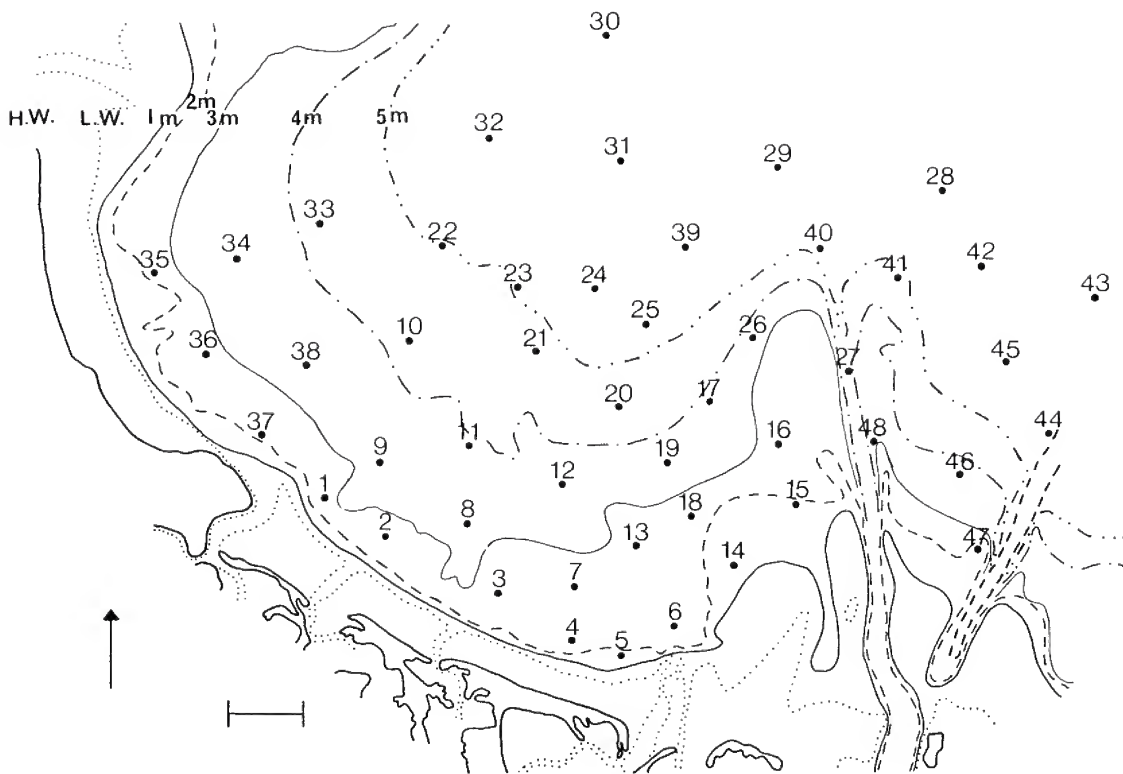


FIG. 2: Bramble Bay, with sampling sites and depth contours. Scale line = 1 km.

each site, and to sample at three-monthly intervals. Sampling at this frequency from the wide area of interest required relatively widely spaced sites and less replication of catches.

An initial trial was conducted with sites ca 1 km apart and with duplicate catches obtained by an 0.1 m² van Veen grab. This revealed clear patterns of species-groups within site-groups, and was adopted for subsequent sampling. For the three-month sampling a tolerably restricted study area was selected (sites 1–27) and this gave the series I data. The results suggested that less frequent studies of a wider area would be desirable and hence sites 1–48 were sampled annually—this gave the series II data. The latter were obtained in September because this was the season of highest populations in the previous study (Stephenson, Williams and Cook 1974).

Raphael (1974) should be consulted for the source of the depth contours on Fig. 2 (these differ from those of published charts) and for such data as exist on tides, winds and temperatures in the area. There are no worthwhile data on salinities but dilution effects are available indirectly from records of rainfall and from overflow discharges over a weir

on the Brisbane River. Details are given in Raphael (1974), and generalities are included in the present paper.

Information on sediments is contained in Maxwell (1970) but additional data were obtained during the present survey.

Each sample, comprising two catches from an 0.1 m² van Veen grab, was wet sieved on board through a final aperture of 1 mm. The residue was carefully examined for small specimens, particularly of gastropods and bivalves; only if these were present the sievings were preserved and the biota sorted at base.

SEDIMENTS

Sediments were sampled by selecting an aliquot of the grab contents, with precautions against loss of biota. For series I, sediment samples were collected thrice (June 1972, Dec. 1972, June 1973) and for series II, at each September.

After removal of organic matter by sodium hypochlorite solution, proportions of particle sizes were determined by wet sieving. Sieve sizes were (in mm): 2.00, 1.00, 0.50, 0.25, 0.125 and 0.063 and

the corresponding fractions are described as: gravel (= shell grit), very coarse sand, coarse sand, medium sand, fine sand and very fine sand respectively. The fraction not retained by the 0.063 mm sieve is referred to as mud.

Throughout there were considerable and apparently random variations between successive samples at a given site; these are believed due to the hand selection of samples from the grab. The upper part of the sample was generally coarser than the lower, and an excess of either would explain the results obtained.

The percentages of each sediment fraction at a given site were averaged and patterns were sought. The most meaningful are based on gradings of the percentages of mud, and of very coarse sand plus gravel respectively. The mud gradings adopted were: high $>75\%$, medium 50–75%, and low $<50\%$, and results are shown in Fig. 3. The coarse sediment gradings based on breaks in the data were: high $>13\%$, medium 7–11%, and low $<7\%$, results are shown in Fig. 4.

The mud distribution shows two tendencies: increase of muddiness with depth, and shorewards

extension of the more muddy areas opposite and slightly west of the main sources of land drainage. The latter are apparent off the Brisbane River and Cabbage Tree Creek. Opposite Serpentine Creek the effect is more localised and only the medium mud zone is involved.

The distribution of the coarser sediments presents an irregular pattern. There tends to be less coarse sediment in the offshore sites, and there are patches, generally isolated, with high content of coarse sediment. The coarse fractions mostly comprise dead bivalve shells and these areas of concentration presumably relate more to biotic distributions in the past than to hydrographic patterns in the present. It is of interest that dredging of shell grit for commercial purposes occurs in the area, but is shoreward of the main concentrations of coarse sediment (see Raphael 1974, fig. 4).

BIOTIC DATA

IDENTIFICATIONS: These were made in part by comparison with reference collections from previously published benthic studies in Moreton Bay

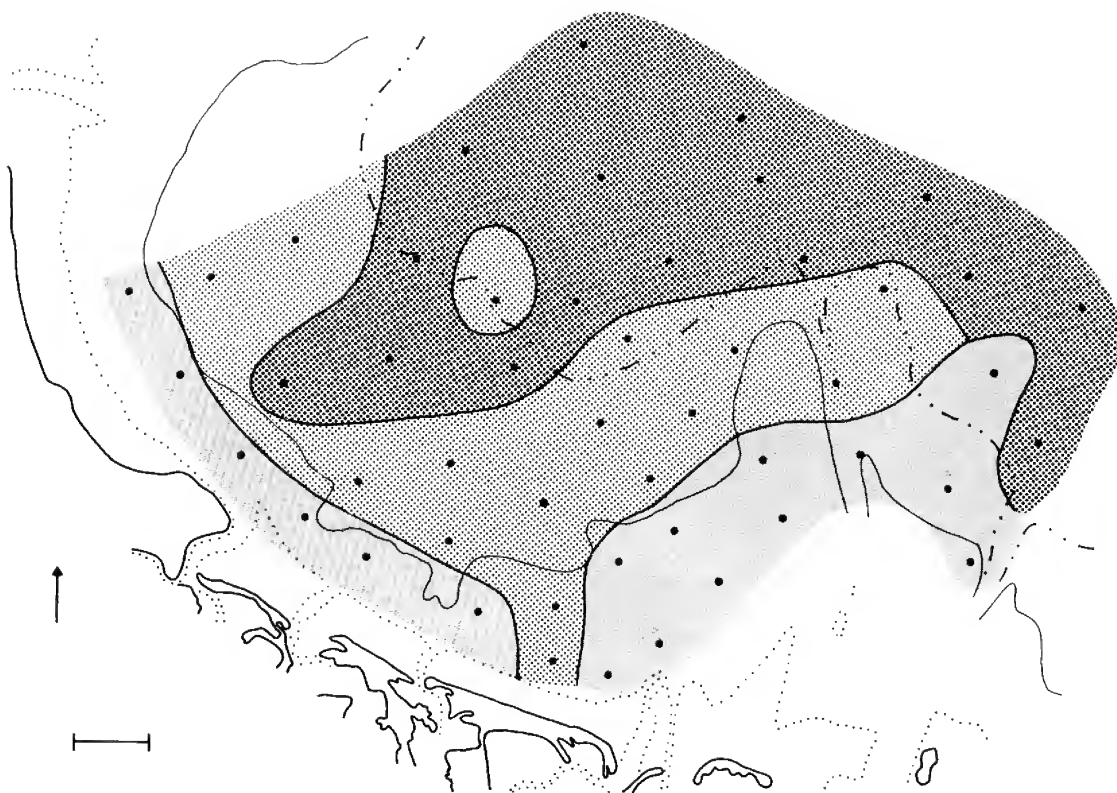


FIG. 3: Distribution of mud in sampled area. High proportion (mean % >75), coarse stipple; medium (50–75%), medium stipple; and low ($<50\%$), fine stipple. Scale line = 1 km.

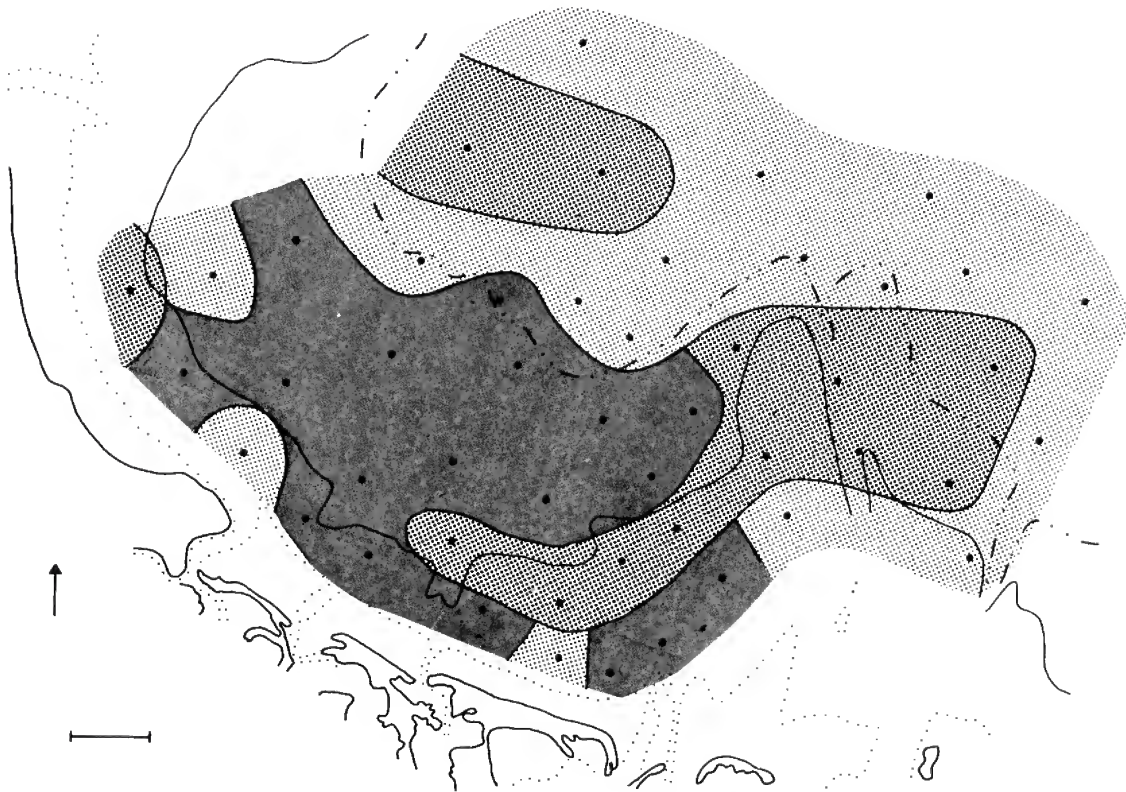


FIG. 4: Distribution of coarse sediments (very coarse sand plus gravel = shell grit). High proportion ($>13\%$) coarse stipple, medium (7–11%) fine stipple, and low ($<7\%$) medium stipple. Scale line = 1 km.

(Stephenson, Williams and Lance 1970; Stephenson, Williams and Cook 1974). Other reference collections (like the above housed in the Queensland Museum), were made by kind assistance from the following: Dr P. Hutchings, Australian Museum; polychaetes (terebellides and ampharettids); Mr B. M. Campbell, Queensland Museum; crabs: Dr C. R. Smalley, Zoology Department, University of Western Australia; alpheidids: Dr W. F. Ponder, Australian Museum, Sydney; some gastropods: Dr A. N. Baker, National Museum, New Zealand; ophiuroids: Dr P. Mather, Queensland Museum; tunicates.

Numerous species have incomplete identifications and at least one taxon is known to be polyspecific; 'tunicate 1' comprises both *Molgula mollis* Herdman and *Cnemidocarpa floccosa* Sluiter.

NON-RECORDINGS: Grabs are inefficient collectors of penaeid prawns and benthic fish, and the few specimens obtained were not recorded.

Dead material was excluded as were empty tubes of polychaetes. *Chaetopterus variopedatus* was an

exception because intact specimens were not obtained; when the tubes appeared to have been inhabited recently, two tube-ends were recorded as one individual.

SPECIES OBTAINED

Raphael (1974) listed 182 species in her shorter survey; 4 additions were recorded in the three seasons of extension. In the comparable Peel Island survey of Stephenson, Williams and Cook (1974) roughly double this number was obtained (420 species) and a current study by Stephenson, Cook and Newlands (MS) records about 450 species from Middle Banks in Moreton Bay. Using a small grab in the Serpentine Creek area over five seasons of sampling, Stephenson and Campbell (in press) obtained ca 90 species, roughly half the present number.

Of the 182 species listed by Raphael (1974), polychaetes contained the largest number of species (39%) followed in decreasing order by bivalves (27%), arthropods (17%), echinoderms (6%), gast-

ropods (4%) and chordates (4%). These percentages are tolerably close to those made at Peel Island by Stephenson, Williams and Cook (1974).

Comparisons of individual species with those obtained in other local surveys are difficult due to incomplete identifications. The closest available comparison is to the Peel Island study, with 70 species known to be common.

METHODS OF ANALYSES

The account below excludes discussion of choice between most of the alternative methods which are available (see Clifford and Stephenson 1975). We have not followed the pioneer 3D study by Williams and Stephenson (1973) for reasons partly given in Stephenson, Williams and Cook (1974) and elaborated in the Discussion.

The data form two different three-dimensional matrices with dimensions s (species) $\times q$ (quadrats or sites) $\times t$ (times). The most convenient method of handling 3D data is to summate over one of the dimensions to produce three 2D matrices of $q \times t$, $s \times q$, and $s \times t$ respectively.

The $q \times t$ matrix as derived directly contains the summated numbers (N) of all species in each sample. Various other forms of $q \times t$ data are readily available. By reducing the recordings of species-in-samples to binary form we obtain the number of species (S) in each sample; this gives a simple measure of diversity per sample. More sophisticated measures are available and we have also used the Shannon diversity, (D) per sample ($N \log N - \sum n \log n$), and also per individual (H^1) expressing these to log base 10. For these four $q \times t$ matrices, recordings of all species are incorporated.

For the remaining analyses, there are advantages in reducing the number of species to consider. Raphael (1974) used different numbers of species for series I data (43) and series II data (51) basing the reductions upon ubiquity considerations. In the present case, in theory we used the same species for both analyses, employing the 81 species with recordings of 10 or more individuals in the total data (231 samples). In fact the species used in the two analyses differed slightly because a few species present in one series of data were absent in the other. The species considered are given in the Appendix. Where only a single species of a genus is there listed, it is referred to in the text by generic name only.

From the $s \times q$ matrix by classification we can obtain site-groups and species-groups on data summated (or averaged) over the times of sampling. From the $s \times t$ matrix by classification, we can

obtain time-groups and species-groups on data summated over all sites. These groupings, based on overall tendencies are of particular value in the context of the present study.

The techniques used in the present case following data reduction were: (a) prior to classification of entities (sites or times), transform recordings by using $\log_{10} (n + 1)$; (b) prior to classification of species, standardise by totals the transformed values; and (c) classify entities and species in both cases using Bray-Curtis dissimilarity measure and group-average sorting.

For easier interpretation of two-way tables, entities (i.e. sites or times) within entity-groups and species within species-groups were arranged by their sequential numbers.

Perusal of the two-way tables indicates that species-groups and their constituent species characterize certain entity groups by occurring there in greater numbers than elsewhere. In a few cases there is 'negative' characterizing by the occurrence of smaller numbers. As stated elsewhere (Stephenson and Dredge 1976) if these characterizations are effected purely by visual inspection of the data there are risks of subjectivity, while if we use statistical tests of the significance of differences these are open to criticism. Because data are near-optimally grouped we are not comparing random samples. As in the previous paper (Stephenson and Dredge 1976) we use the mechanics of certain statistical tests because they appear to follow closely the conclusions reached by visual inspection of the data. We avoid throughout use of the word 'significantly' and use instead 'noticeably' or 'outstandingly'.

Tests were at two levels, the first were for 'scanning' purposes and to determine whether or not entity-group means appeared different. (It should be noted that in the case of time-groups, each entity was taken as forming a group.) In general χ^2 tests were employed using 'raw' (untransformed) summated values. The test was extended below its legitimate limits of *c.* 5 per group (Sokal and Rohlf 1969, p. 565) because it is being used purely for indicative purposes.

When entity-groups appear different by χ^2 testing, there may still be such inter-group variation that the differences are not 'real', hence at a second level the more stringent *F* test was employed, with prior transformation of data using $\log_{10} (n + 1)$.

The results are expressed in terms of noticeability of difference, with HN the equivalent of < 0.01 probability and N of < 0.05 probability as these levels would be applied in usual significance testing. It should be stressed that the true noticeability will

be less than that ascribed because the data have been summated along one of the axes of the 3D matrix, and variation in that axis has been suppressed.

RESULTS

The series I and series II data are separately treated.

SERIES I (27 sites, 7 times)

QUADRATS \times TIMES DATA

The four matrices involving values of N , S , D and H^1 are conveniently approached by summations to give quadrat means and times means—these are given in Table 1. Heterogeneity in the data is of interest and variances of the tabulated means are also given in Table 1, together with the within quadrat and within times variances of N .

Populations (N values) and their variances are highest in quadrats 1, 4, 5, 6 and 14 and in times 5, 6 and 7. The high values and high variances are due to isolated extremely high values as follows: quadrat 1 times 6 and 7, $q4\ t6$, $q5\ t5$ and $t7$, $q6\ t6$ and $t7$, and $q14\ t1$ and $t6$. While these population values are 'patchy' there are clear hints of patterns in this patchiness: the high values are in the inshore sites and mostly in the later sampling periods.

Variances in N values in quadrats and in times are heavily biased by the above outstandingly large sample populations. Thus by excluding the above nine results (ranging from 991 to 4581) the overall variance is reduced by 98%. These high values also contribute largely to the variance interaction of quadrats and times which is 74% of the total variance in the N matrix.

Spearman rank correlation coefficients were derived for various pairs of the columns in Table 1 with results in Table 2.

The high positive correlation for quadrat values between N and D implies that diversities per individual are more meaningful than diversities per site. H^1 values are positively correlated with S , the number of species per site, and negatively correlated with the populations per site.

The correlations for times are not significant in any of the cases. It should be noted that the times interrelationships and quadrat interrelationships did not follow similar patterns. Thus in the times data S and D showed a high positive correlation and also N was positively and not negatively correlated with H^1 .

Considering the H^1 values, variances between sites (0.045) are much greater than the variances between times (0.003). All inshore sites give low H^1

TABLE 1: ANALYSIS OF $q \times t$ DATA

Means and variances of N ; means of S , of D and of H^1 in quadrats and in times. Variances of means are also given. All values rounded.

QUADRATS

Quadrat No.	Mean N	Variance N	Mean S	Mean D	Mean H^1
1	829	2842922	7	62	0.45
2	110	5044	9	52	0.51
3	145	5452	10	63	0.55
4	215	150166	10	61	0.46
5	1002	2660803	11	109	0.28
6	452	448781	12	92	0.44
7	28	135	15	31	1.07
8	61	3219	12	33	0.66
9	24	643	8	14	0.75
10	25	175	11	24	0.91
11	45	348	15	38	0.88
12	33	457	13	31	0.93
13	31	256	13	30	0.95
14	506	407509	10	36	0.48
15	33	333	12	25	0.84
16	43	525	15	42	1.02
17	47	907	10	26	0.62
18	53	536	13	40	0.78
19	66	4828	18	55	0.95
20	64	5166	12	38	0.73
21	82	5451	12	44	0.64
22	46	261	16	48	1.01
23	103	7356	16	81	0.83
24	87	1372	15	61	0.85
25	91	2412	14	61	0.69
26	38	1451	15	33	0.98
27	19	141	9	15	0.80
Overall mean	158.4		12.2	46.1	0.740
Variance of means	62169	—	7.67	511	0.045

TIMES

Time No.	Mean N	Variance N	Mean S	Mean D	Mean H^1
1	130	60565	14	53	0.69
2	102	16168	14	51	0.77
3	107	12646	16	66	0.80
4	53	922	9	30	0.63
5	199	767666	10	31	0.80
6	367	908480	13	57	0.76
7	150	115420	9	37	0.73
Variance of means	10495	—	7.81	193	0.003

TABLE 2: SPEARMAN RANK CORRELATION COEFFICIENTS FOR DATA IN COLUMNS OF TABLE 1. (H.S. < 0.01, N.S. > 0.05)

	<i>N</i> cf. <i>D</i>	<i>S</i> cf. <i>D</i>	<i>S</i> cf. <i>H</i> ¹	<i>N</i> cf. <i>H</i> ¹
Quadrat means	+0.86 (HS)	+0.11 (NS)	+0.66 (HS)	-0.77 (HS)
Times means	+0.25 (NS)	+0.79 (NS)	+0.38 (NS)	+0.23 (NS)

values (sites 1-6 and 14) and there is also a low H^1 value at time 4 (March 1973). This coincides with the lowest populations.

Further discussions of the $q \times t$ data are deferred pending analysis of the $s \times q$ and $s \times t$ matrices.

SPECIES \times QUADRATS DATA

SITE-GROUPS: The dendrogram of site-groupings (Fig. 5) shows a near trichotomy into three unequal groups, the largest group then giving two small and two larger groups. By accepting the above we derive a 7-site inshore group (*I*), a 7-site middle group (*M*) and an 8-site offshore group (*O*), plus five sites in three groups. These sites were allocated to one or another of the three main groups in the order of sites 16, 18, 27, 8 and 9 on the basis of Bray-Curtis comparisons of $\log(n+1)$ data with group means. The three revised groups are:

Inshore (*I*): sites 1, 2, 3, 4, 5, 6, 8, 9, 14.

Middle (*M*): sites 7, 10, 11, 13, 15, 16, 18, 19, 26, 27.

Offshore (*O*): sites 12, 17, 20, 21, 22, 23, 24, 25.

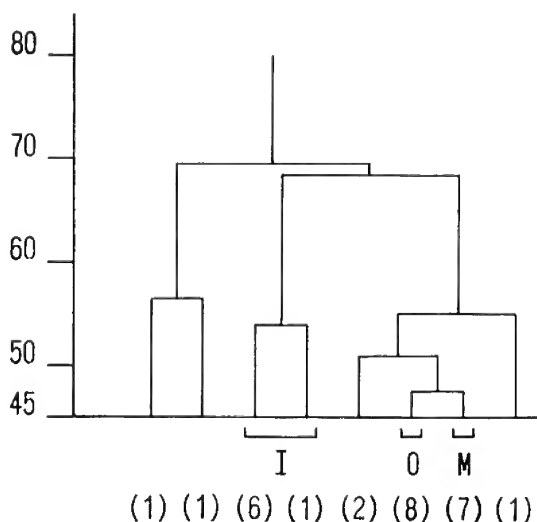


FIG. 5: Truncated dendrogram of classification of 27 sites by species; sites in each group at dendrogram base. *I* sites are inshore, *M* at middle depths and *O* offshore. Sites not in marked groups were re-allocated.

These groups make a coherent topographical picture (Fig. 6). Thus they conform to the extrinsic attribute of proximity; they are also the groups giving the maximum number of outstanding species (i.e. maximum conformity to intrinsic attributes).

SPECIES-GROUPS: The eleven groups originally accepted are shown by dendrogram in Fig. 7. They involved accepting lower dissimilarity levels within the larger groups.

F tests were employed (on transformed data) species by species to determine which had noticeably different values in the three site-groups. In several cases where using three groups failed to show differences one group was tested against the two others and differences were then noticeable. Species which conformed to these tests and those which do not are considered separately. The former comprise 53 of the 79 species in the analysis.

Species-groups with a majority of species conforming to the 3 site-groups: Five groups are involved and these with their constituent species are listed below: non-conforming species are in parenthesis. Site-group characterizations by these species-groups are also given.

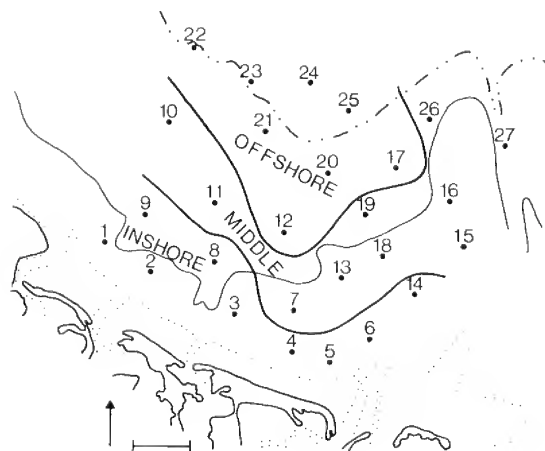


FIG. 6: Site-groups; 27 sites classified by species, after re-allocation of sites. Scale line = 1 km.

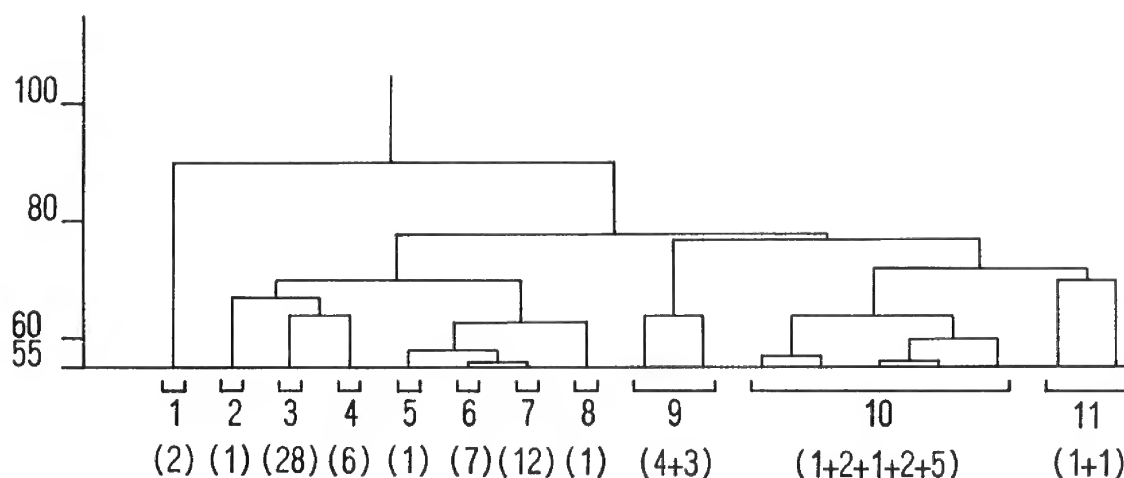


FIG. 7: Series I data; truncated dendrogram of classification of species by sites (species 35 and 75 with nil records, eliminated). At base the species-group numbers used in text, and in parenthesis the numbers of species in each.

Species-group 3: spp. 4, 6, 7, 8, 10, 12, 13, 14, 17, 19, 20, 21, 23, 25, 29, 30, 33, 37, 42, 45, 48, 53, 57, 58, 62, 66 (32, 47). Highest recordings (with minor exceptions) in offshore site-group, lowest in inshore group; designated 'offshore' species.

Species-group 5: sp. 26. Restricted to inshore site-group (and only in certain of these—see later).

Species-group 6: spp. 5, 18, 28, 50, 54, (41, 55). 'Middle' species, highest recordings middle site-group.

Species-group 7: spp. 1, 3, 9, 11, 15, 16, 24, 40, (31, 51, 65, 76). 'Inshore' species.

Species-group 8: spp. 22, 43, 46, 49, 59, 60, 61, 63, 68, 70, 73, 77 (79). 'Middle' species, differences from species-group 6 detailed below.

Summating gives 26 offshore, 17 middle, and 8 inshore species.

While the major site pattern is clearly that of the three main groups, perusal of the data revealed that there are smaller site-groups within them. Thus species 26 (species-group 5) occurs in high numbers in sites 1–4 with low numbers in sites 5–7 and is absent from the remainder. It is a 'sites 1–4' species. Similarly species 45, 47, 58 and 62 (of species-group 1) are a 'sites 21–25' species. These two groups of sites are on the western side of the samples area; 1–4 being western inshore and 21–25 western offshore.

The differences between species-groups 6 and 10 are that in the latter there are proportionally fewer specimens in the inshore site-group, and that the species are concentrated in sites 13, 16, 18, 19, 26, 27, i.e. in the eastern portion of the middle site-group.

Species-groups not conforming to the 3 site-groups: These comprise: group 1, spp. 2, 70; group

2, sp. 67; group 4, spp. 27, 34, 39, 52, 56, and 69; group 8, sp. 80; group 9, spp. 36, 38, 44, 64, 71, 74, 78; and group 11, spp. 72 and 81.

Only one of these species-groups characterizes an extensive and topographically coherent area. This is species-group 4 and all its contained species except one have HN conformity to sites 7–12, 14, 26 and 27. (Apart from one outstandingly large value, the remaining species, 27, also conforms at the HN level.) The area involved approximates to the middle site-group less the sites closest to the Brisbane River, and this general area appears as a discrete site-group in the series II data.

The remaining species-groups have little internal coherence and species are separately considered. Eight species are significantly concentrated at a single site and are designated 'patchy' species. The species with their sites of concentration in parenthesis are 2(14), 27(16), 36(16), 38(27), 44(16), 46(16), 64(16), and 78(16). Six of the eight species are concentrated at site 16.

For the remaining species, it is possible to divide the sites into two groups to obtain noticeably different results, but to do this involves site-groupings which approximate to random scatter throughout the sampled area. The species involved are: 31, 32, 51, 55, 67, 71, 72, 74, 76, 80, 81. These probably include some having pseudo-uniform distribution over the whole area (eg. 31, 32) and others present in too low numbers for patterns to show (eg. 71, 72, 74, 76, 80, 81).

FEATURES OF THE SITE-GROUPS: If the main site-groups are regarded as communities then there are three sets of data on these groups: species composition, sample characteristics from the $q \times t$

TABLE 3: SERIES I DATA (27 SITES); SPECIES \times SITES
A. MEAN NUMBER OF SPECIMENS/m²* OF MORE
ABUNDANT SPECIES (IN SPECIES-GROUPS) IN SITE-GROUPS

Species Group	Species, and code No.	Site-groups (sites in parenthesis)		
		I (1-6, 8, 9, 14)	M (7, 10, 11, 13, 15, 16, 18, 19, 26, 27)	O (12, 17, 20-25)
3	<i>Paratapes</i> , 4	1	16	158
	<i>Amphioplus</i> sp., 6	<1	3	20
	<i>A. lobatus</i> , 7	<1	5	29
	<i>Theora lata</i> , 8	<1	1	10
	<i>Amphitrite</i> , 10	3	6	11
6	<i>Anadara</i> , 5	3	29	6
	tunicate 1, 18	2	5	1
7	<i>Spisula</i> , 1	1347	1	0
	<i>Xenophthalmus</i> , 3	140	38	8
	<i>Terebellides</i> , 9	20	3	2
	<i>Pupa</i> , 11	15	0	0
	<i>Parcanassa</i> , 15	12	2	1
10	oyster 1, 22	0	3	1
	<i>Arca</i> sp. 1, 43	<1	2	<1

* Mean number of specimens per sample, converted to numbers/m² and rounded to nearest unit.

B. MEAN POPULATIONS AND MEAN INDIVIDUAL SHANNON
DIVERSITIES* IN SITE-GROUPS

	Site-groups		
	I	M	O
Mean N/m^2	1858	190	346
Mean H'	0.51	0.92	0.78

* Measured from values per sample of two 0.1 m² grab catches.

C. MEAN NUMBER OF SPECIMENS/m²* OF MORE
ABUNDANT SPECIES IN ALTERNATIVE SPECIFIED SITE-
GROUPS

Sites specified	Species, and code No.	Mean numbers/m ² in:	
		Sites specified	Remainder
1-4	<i>Ophelina</i> , 26	16	<1
	<i>Amphioplus</i>		
21-25	<i>depressus</i> , 45	4	1
	<i>Leptomya</i> , 47	2	<1
22-25	tunicate 3, 19	7	1
	<i>Ophiactis</i> , 59	2	<1
7-12, 14, 26, 27	<i>Petaloproctus</i> , 34	2	<1
	<i>Edwardsia</i> , 39	2	<1

* Mean number of specimens per sample, converted to numbers/m² and rounded to nearest unit.

data, and abiotic features. The first is indicated in the 2-way coincidence table (Table 3A) in which only the most abundant species in each species-group are listed. More briefly the inshore group would be described as *Spisula-Xenophthalmus-Terebellides* community, the middle group as a *Xenophthalmus-Anadara-Paratapes* community and the outer group as a *Paratapes-Amphioplus lobatus* community.

Comparable data on the species which characterise alternative site-groupings are given in Table 3C. Data from the $q \times t$ matrices are given in Table 3B. They comprise mean values of N converted to individuals/m² and mean values of individual diversities (H'). This table shows that the inshore community has the highest mean population but lowest individual diversity; the converse is true of the middle community.

Perusal of Figs. 3 and 6 shows that there is a partial relationship between site-groups and distribution of mud in the sediments. Thus there is near coincidence between the offshore site-group and the area of most muddy sediments, and broadly similar concentric patterns radiating from this area. There are also comparable shorewards protrusions of the medium mud sediments and the middle site-group.

The correspondence between site-groups and mud distribution breaks down in the eastern part of the sampled area. Moreover the eastern site-group does not coincide with the area of high concentration of coarse sediments (see Fig. 4).

There is a similar partial relationship between site-groups and depths. While in the western part of the area, the site-groups occupy different depths, this fails to apply to the eastern part. The simplest overall explanation is that a depth-sediment relationship holds in the western part of the area, but that this is obliterated in the eastern part by some effect of the Brisbane River.

SPECIES \times TIMES DATA

TIME-GROUPS: The dendrogram of time-groupings (Fig. 8) shows two biotically isolated times— t_4 (March 1973) and t_7 (Dec. 1973)—and at a lower level two more coherent groups of times 1, 2, 3, (June–Sept. 1972) and times 5, 6 (June–Sept. 1973) respectively. The acceptance of these groups is at a dissimilarity level of c. 0.25 while acceptance of the three major site-groups in Fig. 5 was at the level of ca 0.45. Clearly while the inter-times group heterogeneity is appreciable it is much less than the inter-site group heterogeneity.

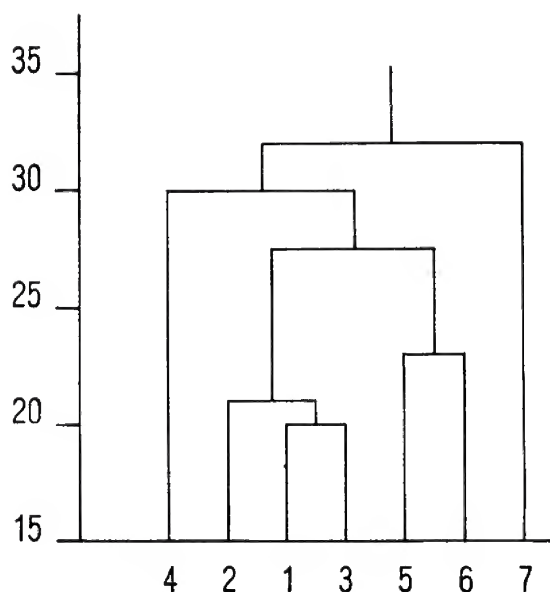


FIG. 8: Series I data; truncated dendrogram of classification of times by species.

If there had been a marked seasonality of the data, time-groupings such as 1, 5; 2, 4 and 3, 7 would have been expected. These did not occur.

SPECIES-GROUPS: The dendrogram gave very unequal groupings; it is not here given because none of the major species-groups were considered as satisfactory from a conceptual viewpoint. 'Satisfactory' species-groupings, as were obtained in the $s \times q$ analyses, are those in which entities (sites or times) are similarly characterized by the species in the group.

The computer-based analyses were replaced by visual and hand calculator analyses. They began by visual scanning the transformed recordings of a given species to select outstanding values. These are usually outstandingly high, in which case times of abundance are selected and times are positively characterized. Occasionally the outstanding values are low, times of scarcity are selected, and the characterization is negative.

The recordings of each species were then divided into two groups—the outstanding values and the remainder—and F tests were then performed on these two groups. Following this, species were grouped by their characterizations of times. Results are given in Table 4.

Table 4 shows that many species (35) positively characterized sequential time patterns, particularly

times 1–3 (14 spp.). Only six species showed seasonal re-occurrences of high recordings. The remaining species have been allocated to four groups as follows:

- (a) Distorted seasonal (positive)—2 spp. Here there is re-occurrence of high recordings to an approximate seasonal pattern. Because there were only four samplings per year and because advance or delay in seasonal peaks may well occur, these may be truly seasonal species.
- (b) Single time—9 positive spp., 6 negative spp. These are referred to later as 'time-patchy' species.
- (c) Nonsensical—9 spp. These had markedly different recordings throughout three sampling periods, and typically high, low and high, giving a 'saw-tooth' graph.
- (d) No times characterized—10 spp. In these there were no outstanding recordings and

TABLE 4: TIME-GROUPINGS CHARACTERISED BY SPECIES; SERIES I DATA

Times	Species characterization	
	Positive	Negative
Sequential 1–3	4, 5, 9, 10, 18, 20, 24, 32, 37, 41, 42, 56, 57, 74	
2–3	28, 61, 74	60
5, 6	1, 7, 22, 26, 38, 69, 76, 81	
1–6	25, 50, 52	
1–4	4, 9	
2–4	48	
3, 4	29, 45, 64	
2–5	15	
6, 7	34, 43, 47	
Seasonal		
2, 6	12, 31, 49	
3, 7	27, 36, 54	
Distorted Seasonal		
1, 2, 6	2	
2, 5	16	
Single time		
1	67, 72	
2	19	
3	21, 59	
4		14, 33
6	71	
7	8, 39, 44	11, 23, 50, 52
Nonsensical	3, 16, 17, 30, 46, 51, 62, 68, 73	
No times characterized (Random)	53, 55, 63, 65, 66, 70, 77, 78, 79, 81	

testing raw values with χ^2 showed no noticeable difference from randomness. They are referred to below as random species.

The time-patchy and nonsensical species (24 in all) may either have rapid changes in populations or, more likely, result from a patchy microtopographical distribution. The random species are all low in the abundance hierarchy, and randomness is likely to be due to small recordings rather than truly stable ones.

FEATURES OF THE TIME-GROUPS: As with site-groups there are three sets of relevant data: species composition, sample characterisation from the $q \times t$ data, and possible abiotic 'explanations'.

The reduced 2-way coincidence (Table 5A) indicates the most important positively characterizing species of these time-groups, while Table 5B shows the population and individual diversity data.

In brief, times 1–3 are a period of *Paratapes*, *Anadara*, *Terebellides* and *Amphitrite*; there are no species positively characterising time 4 only; times 5 and 6 are a period of *Spisula* and *Amphioplus lobatus*; while time 7 is a period of *Theora lata*.

TABLE 5: SERIES I DATA (27 SITES); SPECIES \times TIMES

A. MEAN NUMBER OF SPECIMENS/m²* OF MORE ABUNDANT SPECIES IN GROUPS (FROM TABLE 4) IN TIME-GROUPS

Species, and code No.	Times			
	1–3	4	5, 6	7
<i>Paratapes</i> , 4	101	57	4	5
<i>Anadara</i> , 5	23	10	6	5
<i>Terebellides</i> , 9	17	7	1	1
<i>Amphitrite</i> , 10	11	5	3	2
tunicate 1, 18	5	1	1	1
<i>Spisula</i> , 1	127	28	1082	572
<i>Amphioplus lobatus</i> , 7	9	7	16	8
<i>Theora lata</i> , 8	1	0	0	20

* Mean number of specimens per sample, converted to numbers/m² and rounded to nearest unit.

B. MEAN POPULATIONS AND MEAN INDIVIDUAL SHANNON DIVERSITIES* IN TIME-GROUPS

	Times			
	1–3	4	5, 6	7
Mean N/m^2	563	265	1415	750
Mean H^1	0.75	0.63	0.78	0.73

* Measured from values per sample of two 0.1m² grab catches.

In terms of population density times 1–3 and 7 are about average, time 4 is outstandingly low and times 5 and 6 outstandingly high. Individual diversities are quasi-constant throughout except for a marked low in time 4.

Overall the most dissimilar time is time 4 (March 1973). Comparable studies near Peel Island in Moreton Bay by Stephenson, Williams and Cook (1974), revealed outstandingly low populations in their two March samplings. Moreover the lowest values were in March 1970 which followed a period of normal climate, instead of in March 1971 following the wettest summer (Dec.–Feb.) for 24 years. In the present case March 1972 follows a dry period.

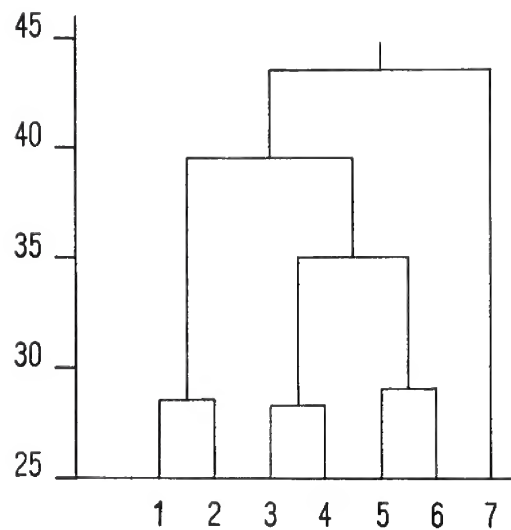
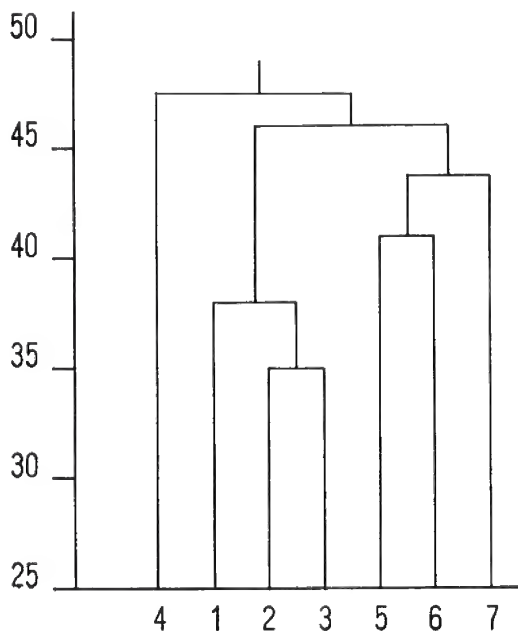
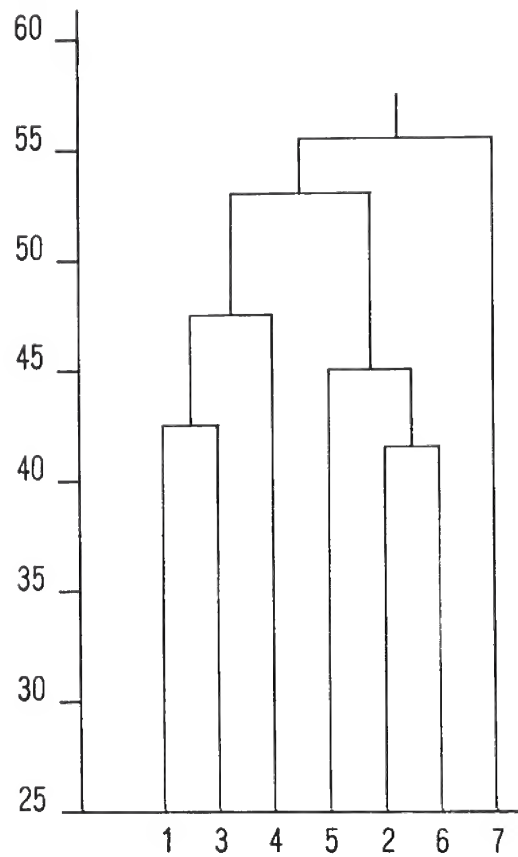
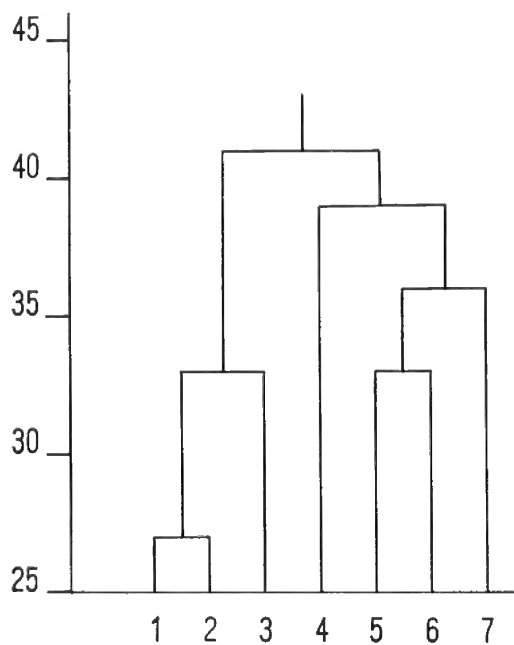
The effect of rainfall would be primarily by run-off from the Brisbane River, and data in Raphael (1974) show less than normal discharge in the Brisbane River for eight of the nine preceding months. Assuming that river run-off is the controlling factor then times 1–3 fall in a period of reduced run-off but one which follows a wetter period (Feb.–May 1972). Conversely times 5 and 6 fall in a period of approximately normal run-off but one following a drier period (June 1972–May 1973). On this basis the difference between times 3 and 7 (Dec. 1972 and Dec. 1973) reflects the low run-off preceding the former, and the approximately average run-off preceding the latter.

The only other continuous abiotic data of seeming relevance to the present situation are of air temperatures. There are no obvious relationships between these data and the time-groups.

FURTHER ANALYSES

Following the above analyses, two others suggested themselves. Both are concerned with shortcomings of the technique of converting a three-dimensional matrix into three two-dimensional ones.

EXTREME SPACE-TIME PATCHINESS: During summation across one of the axes of the matrix, variation along that axis is suppressed. Thus a high recording of a species in a site may be based upon uniformly high recordings in all times or may be based upon an extraordinarily high recording at a single time. Such a value could bias both the $q \times t$ and $s \times q$ analyses. A simple method was used to recognise species showing extreme 'space-time' patchiness by way of a single outstanding recording. The transformed data on each species (79 in all) was considered within its own $q \times t$ (27 \times 7) matrix. The F test was then applied comparing the largest recording with the remainder.



FIGS. 9-12: Series I data: dendrogram of classification of times by species.

FIG. 9: Inshore sites.

FIG. 10: Mid-eastern sites, nearest Brisbane River.

FIG. 11: Mid-western sites.

FIG. 12: Offshore sites.

To determine which results show extreme patchiness we must decide on a probability in relation to the F level. The lowest listed in tables is 0.001, and to accept this would give 73/79 extremely patchy species. Taking five times the F level at the 0.001 value gives the following 25 space-time patchy species: 2, 19, 22, 27, 34, 36, 38, 43, 44, 50, 59, 60, 61, 63, 64, 65, 68, 69, 70, 71, 72, 73, 74, 77, 78, 81.

The species previously judged site-patchy are: 2, 27, 36, 38, 44, 46, 64, 78, and 7/8 of these are in the above list. Of the 15 species previously judged time-patchy only six appear on the above list: 19, 44, 50, 59, 71, 72. It is evident that the present method does have cautionary value, particularly regarding space-patchiness.

The places and times of the space-time patchiness give concentrations as follows: *quadrats* 11, 13, 16, 18, and 19 which are all in the middle site-group and mostly on its eastern side, and *times* 3, 5, 6, 7; these are mostly towards the end of the sampling period.

INTERACTIONS BETWEEN SPACE AND TIME: The usual calculations of variance interaction essayed on a species by species basis, showed that most of the interaction was due to the few, usually single, outstandingly large values as considered above.

Further and more directly meaningful analyses involving interactions were then undertaken and for two reasons: (i) the main heterogeneity is between sites; by operating within site-groups it seems possible that times-groups would be more coherent and (ii) within different site-groups one might expect differences in time-groupings. If the previous argument that variable run-off from the Brisbane River explains some of the results is correct, then the greatest time-dissimilarities should occur in the sites adjacent to it.

The three original site-groups were converted to four by arbitrary division of the middle one and by transfer of one site (12) to the group suggested by its topography. This gave:

Inshore: sites 1-6, 8, 9, 14.

Middle eastern (nearest river): sites 15, 16, 18, 26, 27.

Middle western: sites 7, 10-13, 19.

Offshore: sites 12, 16-18, 20-25.

The four dendrograms of time-groupings within these site-groups are given in Figs. 9 to 12.

The mean percentages dissimilarity at which times separate as individual entities are as follows: inshore 32.6, mid-eastern 44.9, mid-western 39.9, outer 30.5. As expected the site-group nearest the river shows the greatest time heterogeneity. Possibly the river influence extends to the mid-western

region; this shows greater time-heterogeneity than the inshore site-group.

The inshore group shows division by years into time 1-3 and 4-7, and in the midwest there is a somewhat similar picture (times 1-3 and 5-7). The mid-east has a broadly annual picture, upset by a seasonal linkage of times 2 and 6. The offshore area differs from the remainder in having three groupings of successive times, viz: times 1, 2 and 3; 4 and 5; 6.

Species-groupings were examined in each of the above cases. Those produced by the classificatory programme failed to give conceptual sense, as expected and discussed earlier. In the present cases, grouping species by conformity testing likewise failed to give meaningful conclusions. This was because dividing the sites into groups reduced the populations of most species to levels below those at which differences were outstanding. The time-groups were distinguished by summations of tendencies which when considered individually revealed little.

SERIES II (48 sites, 2 times)

QUADRATS \times TIMES DATA

These are only considered in relation to site-groups and time-groups and are detailed later.

SPECIES \times QUADRATS DATA

SITE-GROUPS: The dendrograms of site-groupings (Fig. 13) gives an initial dichotomy; the site-groups so obtained lie offshore and onshore respectively. To obtain the maximum number of conforming species required more homogeneous site-groups; eventually seven major groups were adopted as shown on the dendrogram base. This left two isolated sites, 27 and 14; the former was allocated to the major site-group with greatest biotic affinities, site-group E. Site 14 is very dissimilar from the remainder, due to large numbers of species 2 (*Mesochaetopterus minutus*) and was retained as an isolate. The site-groups thus adopted are map-plotted on Fig. 14.

Site-groups A, B and C, which are tolerably closely linked in the dendrogram, all comprise inshore sites. Group A is the most inshore, B is intermediate and western, C is the deepest of the three and eastern. Site-group G, by dendrogram more distantly related to the above three groups lies nearest to the river mouth and tends to be more offshore than site-group C.

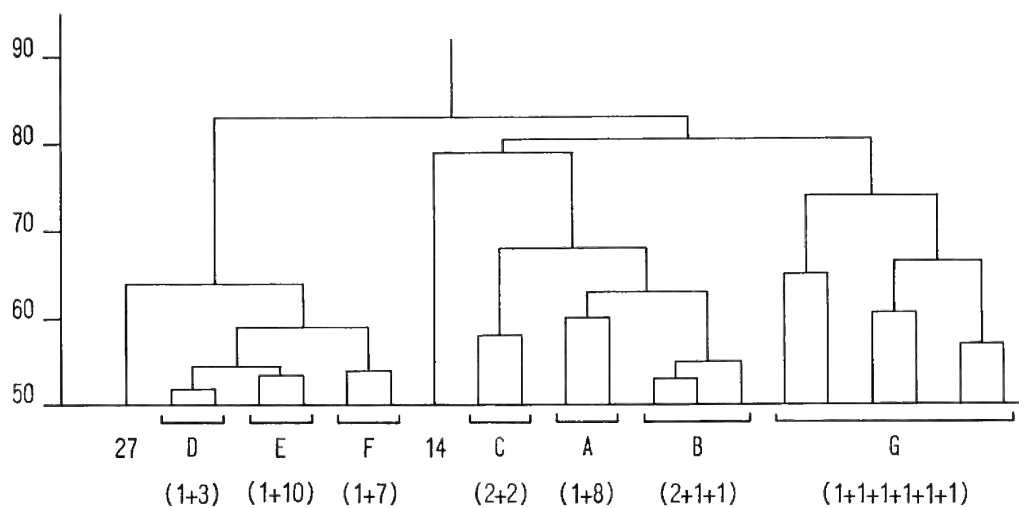


FIG. 13: Series II data (48 sites); truncated dendrogram of classification of sites by species; number of sites in each group in parenthesis at dendrogram base.

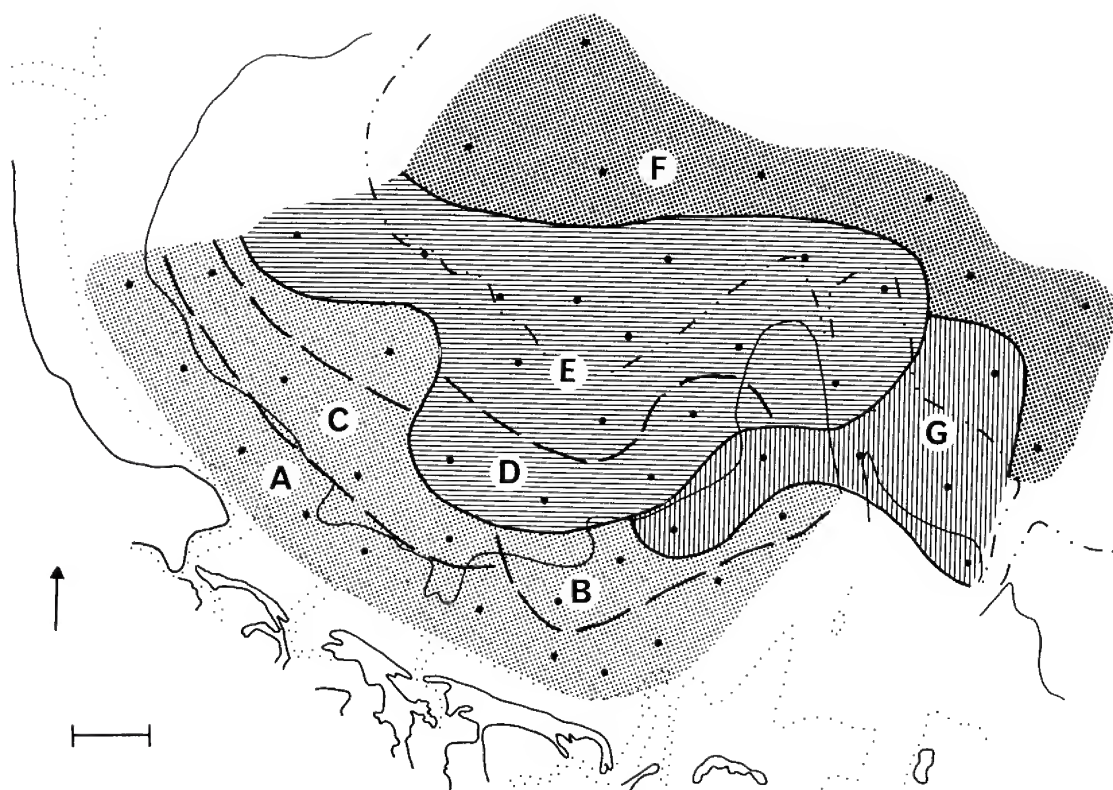


FIG. 14: Site-groups; 48 sites, classified by species after re-allocation of site 27. Scale line = 1 km.

Site-groups D, E and F are closely linked in the dendrogram, especially D and E. Topographically the three form a series with D closest inshore, E intermediate and F offshore. Site-group F extends laterally to off the mouth of the Brisbane River.

In general there is a clear topographic pattern, in which the most obvious relationship is to depth distance offshore. The separation of site-group G seems to indicate a second influence, that of river proximity.

SPECIES-GROUPS: Apart from three isolated species (2, 45, 46) there is almost a trichotomy into three groups. By further division of the larger groups seven major species-groups were obtained (Fig. 15).

F tests were performed to determine which species had noticeably different values in the seven site-groups. Only 30 out of the 69 species in the analysis conformed, i.e. 43%, compared with 67% in the series I data.

This is not because there are now more 'patchy' species concentrated in a single site. There are seven such species; these, with sites of occurrence in parenthesis, are: 2(14), 6(48), 20(45), 37(31), 40(48), 45(47), 46(47). The difference is due to the fact that there are many more 'random' species. This is a reflection of the lower recordings; present data involve four grab catches, while the series I data involved fourteen.

Perusal of the two-way table revealed that in several species-groups there was uniform or nearly uniform positive characterisation of a site-group by a species-group. Species-group I showed concentration in site-group A, (extreme inshore) except for one species (41) with a single outstandingly high value outside the area; species-group IV characterised site-group E; species-group VI showed major concentration in site-group G (near river mouth) and minor concentration in site-group D (adjacent). Species-groups V and VII comprised species with low recordings mostly approximating to random scatter amongst the sites, and there remains species-group III, the largest of all. The most discrete sub-unit comprises species 4, 5, 7, 12, 27, 31 and 38, and these are concentrated in site-group E. The remainder do not consistently characterise any of the site-groups. Perusal of the data suggests that the remaining eleven species (9, 13, 14, 21, 22, 24, 26, 29, 32, 35, 43) characterise an alternative grouping of sites, with concentrations in an area approximately encompassing sites 6, 11, 12, 13, 17, 19, 20, 21, 22, 23, 24, 25, and 26.

FEATURES OF THE SITE-GROUPS: A condensed 2-way coincidence table (Table 6A) summarises the site-group/species-group relationships as regards the commoner species. Perusal of the equivalent table for the series I data (Table 3A) shows many differences; both site-groups and characterising

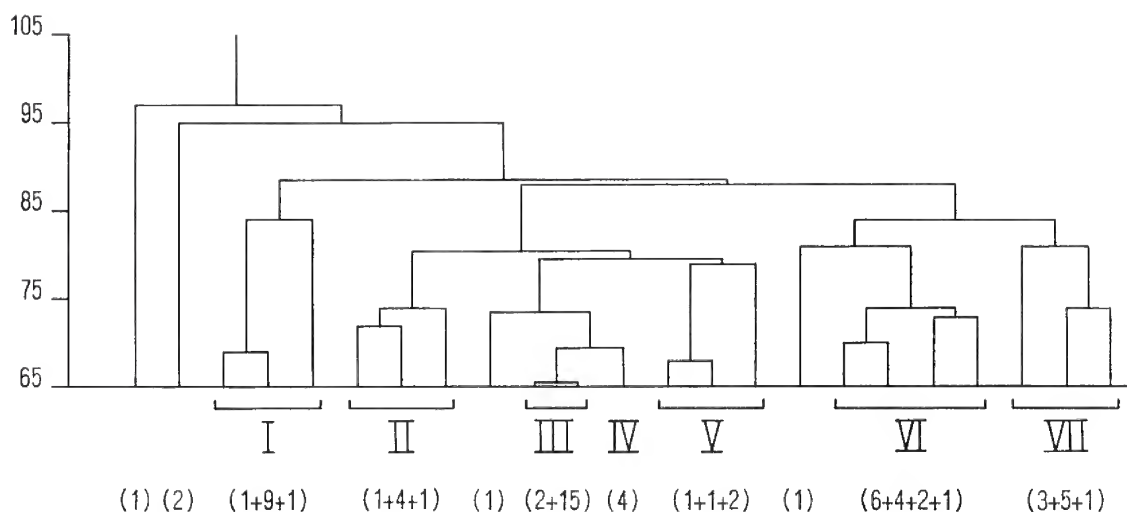


FIG. 15: Series II data; truncated dendrogram of classification of species by sites. At base species-group numbers used in text, and in parenthesis number of species in each.

TABLE 6: SERIES II DATA (48 SITES); SPECIES \times SITESA. MEAN NUMBER OF SPECIMENS/m² OF MORE ABUNDANT SPECIES IN MAIN SITE-GROUPS

Species group	Species and code No.	Main site-groups (sites in parenthesis)						
		A (1-6, 35-37)	B (8, 9, 34, 38)	C (7, 10, 13, 15)	D (11, 12, 17, 19)	E (20 27, 33)	F (28, 32 42, 43)	G (16, 18, 45-48)
I	<i>Spisula</i> , 1	2626	261	1	0	1	0	0
	<i>Xenophthalmus</i> , 3	228	3	10	3	6	0	42
	<i>Amphitrite</i> , 10	27	5	0	0	0	0	0
II	<i>Amphioplus</i> sp., 6	0	2	1	4	5	55	9
	<i>Parcanassa</i> , 15	0	0	0	0	2	14	1
III	<i>Paratapes</i> , 4	1	6	10	53	133	58	2
	<i>Anadara</i> , 5	0	1	2	6	31	57	1
	<i>Amphioplus lobatus</i> , 7	0	0	5	12	31	8	0
	<i>Terebellides</i> , 9	8	4	19	22	15	5	0
IV	<i>Pupa</i> , 11	1	5	3	0	15	0	6
VI	<i>Theora lata</i> , 8	2	5	6	22	1	0	53
	tunicate 1, 18	0	3	2	12	0	0	10

*Mean number of specimens per sample, converted to numbers/m² and rounded to nearest unit.

B. MEAN POPULATIONS AND MEAN INDIVIDUAL SHANNON DIVERSITIES* IN TIME-GROUPS

I	Main site-groups						
	A	B	C	D	E	F	G
Mean N/m^2	2946	361	109	218	332	242	267
Mean H'	0.42	0.66	1.05	0.92	0.82	0.67	0.81

*Meaned from values per sample of two 0.1 m² grab catches.

species-groups have changed and this makes detailed comparisons difficult. If a choice is to be made between the species/site results of the two studies, that from the more extensive series I data is preferred.

Of the abiotic factors which might influence the series II site-groups, sediment relationships are obscure (compare Figs. 3 and 4 with Fig. 14); an effect of the Brisbane River is clear; but the main factor appears to be related to distance offshore. Whether this is due to depth, dilution, turbidity, or some other factor is unknown.

Table 6B shows population densities and mean individual diversities within the site-groups, and as before there is an inverse relationship. Again the most inshore group (site-group A) has the highest populations. The groups at intermediate depths differ from each other as regards population density and diversity: lowest populations and highest diversities are in the central somewhat inshore site-group C; site-group G nearest the Brisbane River has roughly average values for both; and the most offshore site-group F has somewhat lower populations and higher diversity than average.

SPECIES \times TIMES DATA

With only two times, the times classification is a single dichotomy. This is at a dissimilarity level of 21%, considerably less than the dissimilarity between the two Septembers based only on 27 sites (31%). The decrease is due to the inclusion of sites which are more offshore and/or further from the Brisbane River.

With only two times, there is no variability of species-in-times, and the F test cannot be employed. Use of the χ^2 test on raw numbers (summed over all sites) showed 22 species with higher populations in 1972, 18 with higher values in 1973, leaving 39 without noticeable differences.

Total populations of all species summated were lower in time 1 with an average of 408 individuals/m² compared with 1346 in time 2. Mean individual diversities were 0.74 and 0.67 respectively.

DISCUSSION

This involves three main topics, (a) methods, both sampling and numerical, (b) matters related to airport construction, and (c) general matters related to communities, productivity, etc.

METHODS

SAMPLING METHODS: Stephenson, Williams and Cook (1974), established certain desiderata based on their work at Peel Island which could not be followed in the present study. These were that stations should be c. 0.25 km apart and that there should be quintuplicate grab catches on each occasion. In the present work samples were c. 1 km apart and catches were in duplicate.

The results obtained have in general shown that the wider spacing of sites was acceptable in that the site-patterns obtained have been topographically coherent and meaningful. Only one site (14) has not been closely linked to its neighbours and this was due to patchy distribution of species 2 (*Mesochaetopterus minutus*).

Nevertheless problems remain over the spacing of sites. On each sampling two catches were made in close proximity but on a subsequent occasion the pair were likely to be up to 25 m from the originals. If a species is patchily distributed then on one occasion it might be collected and on another missed. In brief, microtopographic patterning could give the appearance of a marked seasonal change in numbers. A sufficient number of species showed 'saw-tooth' types of seasonal change to suggest that this was occurring. This casts doubts on the reality of the supposed time changes of the remaining species. Nevertheless a sufficient number of species give 'sensible' results for the time changes described to be regarded as real.

Further evidence for this was obtained by analysis of time-changes within sub-units of the sampling area. Here the data are weaker because summations involve fewer sites, but the time analyses result in somewhat greater conceptual sense.

NUMERICAL METHODS: Apart from a paper written after but published before the present account (Stephenson and Dredge 1975) the last published account of classifying multidimensional data which we are aware of was by Stephenson, Williams and Cook (1974). This involved variance measures of dissimilarity, whose magnitudes are very sensitive to the type of data transformation which is used; also it failed to give optimal species-groupings.

Since this, work experience has been gained in a variety of analyses of two-dimensional data by the senior author in concert with other workers. These include unpublished work by Godfriaux and Stephenson, preliminary reports upon the present work by Raphael and Stephenson (1972), and manuscript work by Stephenson *et al.* on wastewater outfalls at Los Angeles. Throughout, this

work has shown that for benthic analyses the Bray-Curtis measure of dissimilarity has advantages. Used on raw data dissimilarities are possibly too strongly biased towards the numerically abundant species and it is generally desirable to use transformed data. In the earlier work quoted above (Godfriaux and Stephenson, Raphael and Stephenson) the \sqrt{n} transformed was used, and this was also employed by Raphael (1974) in her thesis. Stephenson *et al.* (in MS) used the cube root transformation with the Bray-Curtis measure, but in the present work the more stringent $\log(n+1)$ transformation has been employed. It follows precedents created by Field and Robb (1970), Day, Field and Montgomery (1971), Field and Macfarlane (1968), Field (1971) and Christie (1974). However the choice was mostly influenced by results not yet published concerning the effects of a major flood on the present biota.

Following Boesch (personal communication), the preliminaries to the present work, and the manuscript work by Stephenson *et al.* for species-groupings we have used the proportionality of a species-in-sites instead of the absolute recordings. (Actually the proportions of transformed values were used.) This has resulted in better groupings of species with similar site recordings and has been an improvement compared with the variance technique of Williams and Stephenson (1973), and of Stephenson, Williams and Cook (1974). Meanwhile from a more theoretical aspect Dale and Anderson (1973) have already shown that optimal groupings of sites and of species do require different techniques.

In the present method as in the original 3D treatment of Williams and Stephenson (1973) we summated along a specified axis of the matrix to produce three two-dimensional matrices of $q \times t$, $s \times q$, and $s \times t$ respectively. As a consequence in each matrix variability in the other axis is lost and a single large recording of a species in a sample can influence all three of the two-dimensional matrices. A technique has been developed to locate and 'give warning' of such single outstanding values. It involves an *F* test (on transformed data) in which the largest value is compared with the remainder. In the present work 'patchy' species were also sought by heuristic examination of the results of site analyses and of time analyses. There was general agreement between the test and the conclusions drawn from site analyses.

In one respect the present methods revert to those of Stephenson, Williams and Cook (1974). This is in the use of the *F* test for investigating the conformity of species to entity-groups (i.e. site-groups or time-groups). We appreciate that the

data to be tested have been grouped by near-optimal techniques and that the basis for testing of significance is hence destroyed. However we suggest that this test still has conceptual value and has a close relationship to the intuitive bases of data scanning. Because it takes more strict account of within-group variation, it seems preferable over other tests. Throughout it was used at different levels in the classificatory hierarchies, and the levels finally selected gave the maximum number of conforming species.

Although the present methods have proved generally satisfactory, problems remain over species-groups: species within a group sometimes fail to conform in a uniform way to the entity groups. In some cases this has proved conceptually helpful as indicating alternative site-groupings. Such groupings have been sought unsuccessfully in two previous studies (Stephenson, Williams and Cook 1974, Stephenson *et al.* in MS).

In general species-grouping using sites data has proved satisfactory, but species-grouping with times data has not. The problems have been discussed earlier and have been partially resolved in the present paper by intuitively based analyses. As yet these defy formalization to the level of computer programming.

RELATION TO AIRPORT CONSTRUCTION

To predict changes in the Bramble Bay benthos due to airport construction requires (1) that there should be recognisable and quantifiable patterns in the biota before construction, (2) an estimation of which patterns are likely to change due to overall human activities, and (3) estimation of the particular effect of airport construction.

Site-patterns have been obtained with both the series I data (27 sites, 7 times) and the series II data (48 sites, 2 times). As might be expected these are not identical, but they do show broadly similar tendencies. It is of especial interest that the boundaries of the middle-depth site-groupings bulge shorewards opposite Serpentine Creek. For this there are two possible explanations, either a specific effect of Serpentine Creek, or the fact that it is an area roughly midway between two larger systems of freshwater drainage. Whichever is involved, the reduction in run-off from Serpentine Creek following airport construction is likely to cause changes. Present data show the area has relatively high diversity but relatively low population density.

Only the series I data produced time patterns worthy of further consideration. These show that there are noteworthy time changes and that these

involve very little repetition from the seasons of one year to those of the next. Instead certain species characterise the total area for a certain period (e.g. 9 months) and are superseded by other species. Time changes are most marked in the area nearest the Brisbane River. They indicate an annual change-over in biota in the inshore sites and an approximately six-months change-over in the offshore sites. It was suggested that variable run off of freshwater was the major cause of these temporal changes and if this is so, occlusion of Serpentine Creek might lead to increased temporal stability. The general literature on biotic diversity suggests that this would result in an increase in diversity. However this is far from certain and the reverse might well be true (see Stephenson, Williams and Cook 1974; Clifford and Stephenson 1975).

It is clear that investigations of considerable duration, much in excess of the proposed two years, would be required before adequate predictions could be made concerning temporal changes during 'normal' conditions. The flood of January 1974 terminated such 'normality' and as will be shown in a later paper produced dramatic effects.

Airport construction will be only one of many human influences which will operate in the area. Other factors include:

- (a) Shell dredging. This currently occurs at site 5 and inshore of sites 6 and 14; it may well extend in the future.
- (b) Prawn trawling. This occurs seasonally throughout the area except for the inshore sites. Annual variations in trawling intensity in the area have not been adequately quantified.
- (c) Port construction. Major construction at Fisherman Island with filling of the Boat Passage seems probable. This is likely to cause marked changes in the suggested 'Brisbane River' effect.
- (d) Reduction of pollution. Industrial pollution of the Brisbane River and Cabbage Tree Creek is currently being reduced, and discharge of untreated sewage is likely to be reduced in the future.

Amidst the welter of probable changes due to man, and with the ever-present possibility of another devastating flood, predictions of the effects of airport construction can only be tentative.

GENERAL MATTERS

Most workers on benthic biotas still feel constrained to express their results in terms of benthic communities, although it has been shown that the

community concept is complex and possibly confusing (see Stephenson 1973; Clifford and Stephenson 1975). In the present case it is not possible to accept the restraints of Petersen (1914) and limit the species characterising the sites to those with constantly high populations. The populations of virtually all species show changes during the sampling periods.

By taking averages over all times, groups of sites characterised by groups of species can be revealed. In the 27 sites analysis the most important of these are: inshore a *Spisula-Xenophthalmus-Terebellides* group; in the middle a *Xenophthalmus-Anadara-Paratapes* group; and offshore a *Paratapes-Amphioplus lobatus* group. In the 48 sites analysis there is greater topographic resolution but characterization of site-groups by species-groups is less distinctive. The inshore species-group is now *Spisula-Xenophthalmus-Amphitrite* and the offshore area group is *Paratapes-Anadara-Amphioplus lobatus-Terebellides*. These "communities" bear scant relationship to that of the adjacent area of Moreton Bay in the dredge study by Stephenson, Williams and Lance (1970). The difference is mainly due to the different collecting methods, as already noted in the Peel Island study (Stephenson, Williams and Cook 1974). There is a somewhat closer relationship to the characterizing species which Hailstone (1972) noted in a dredge study of the lower Brisbane River. Hailstone obtained large numbers of *Spisula* with *Parcanassa* and other species in shallow sandy-mud sediments, while *Anadara* characterized mid-channel sites with muddy sand. MacIntyre (1959) in his study of Lake Macquarie in New South Wales also obtained large numbers of several of the present species, particularly *Anadara*, *Paratapes*, and *Amphioplus lobatus*. Black (1971) noted that *Spisula* is common from sandy sites in Port Phillip Bay, Victoria, and it is listed from three regions in that bay by Poore and Rainer (1974). Other species of *Spisula* are well-known characterizing species elsewhere (see Thorson 1957) and a *Xenophthalmus* community is known from sandy grounds in the Persian Gulf (Thorson 1957).

Possibly the closest parallel with the present results is the New Guinea study by Stephenson and Williams (1971). Here there was an *Amphioplus* and a *Mesochaetopterus* 'community' both in a warm water situation under estuarine influence. The study by Stephenson, Williams and Cook (1974) is closest to the present work in times of sampling and analytical methods but the abundant species characterising site-groups have little in common.

Present results show that the densest populations are inshore, and the mean value for one data set is

1858 specimens/m² and for the other 2946. These values compare with 16–764 by Chukchin (1963) in eastern Mediterranean at depths of 100–200 m; 102–255 by Kuznetsov (1963) in the northern Pacific at depths to 500 m; 740–5515 by Wigley and McIntyre (1964) in the western North Atlantic at 40–366 m; and 32–1193 by Christie (1974) in South Africa at depths to 50 m. Values obtained by Sanders *et al.* (1965) were much higher (to 21263/m²) but they used a finer mesh sieve (0.42 mm). It is unfortunately not possible to compare present densities with those of the current extensive investigations in Port Phillip Bay, Victoria. Poore and Rainer (1974) deal only with molluscs and give an overall mean of 1457 individuals/m². This suggests that densities involving all species will be distinctly higher than those of the present study.

In the inshore sites, with the densest populations, it appears that there are marked annual changes in populations. This must result in high productivity of the benthic macrofauna; in absence of biomass determinations its magnitude is unknown. In the most offshore site-group in the 27 sites data, populations are lower and average 346 animals/m². Here however there are indications of a marked biotic change every six months. Again the macrofauna productivity must be of a high order.

Possibly the most interesting results of the present survey concern the time changes in biota. They confirm the opinion stated by Stephenson, Williams and Cook (1974) and by Clifford and Stephenson (1975) of the extremely doubtful value of many of the environmental impact statements involving benthic organisms.

The time investigations, cautiously interpreted because of possible microtopographical patterning, still stress the transitory nature of some of the species and the marked fluctuations in the populations of others. They give pointers to matters of both practical and fundamental importance. From a practical viewpoint, if environmental conditions are not too greatly disturbed, it appears that one biotic assemblance can readily replace another. It can hence be regarded as a buffered biotic system; provided airport construction does not greatly disturb conditions one might expect the buffering to operate tolerably quickly. Another and somewhat different aspect of 'buffering' in benthos has been noted in a recent paper involving a 4-year study by Buchanan, Kingston and Shearer (1974).

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APPENDIX

Species (and their systematic group) in order of abundance in all samples ($27 \times 7 + 21 \times 2$); only species occurring 9 times listed. Code number is given in first column and total population in last column.

1	<i>Spisula trigonella</i> (Lamarck)	Pelecypoda (Mactridae)	19318
2	<i>Mesochaetopterus minutus</i> Potts	Polychaeta (Chaetopteridae)	3367
3	<i>Xenophthalmus pinnotheroides</i> White	Decapoda (Pinnotheridae)	2457
4	<i>Paratapes scordalus</i> Iredale	Pelecypoda (Veneridae)	2238
5	<i>Anadara trapezia</i> Deshayes	Pelecypoda (Arcidae)	532
6	<i>Amphioplus</i> sp.	Echinodermata (Ophiuroidae)	520
7	<i>Amphioplus lobatus</i> (Ljungman)	Echinodermata (Ophiuroidae)	456
8	<i>Theora lata</i> Hinds	Pelecypoda (Tellinidae)	358
9	<i>Terebellides stroemi</i> Sars	Polychaeta (Terebellidae)	323
10	<i>Amphitrite rubra</i> (Risso)	Polychaeta (Terebellidae)	283
11	<i>Pupa fumata</i> (Reeve)	Gastropoda (Acteonidae)	221
12	<i>Theora</i> sp.	Pelecypoda (Tellinidae)	216
13	<i>Amphipholis loripes</i> Koehler	Echinodermata (Ophiuroidae)	204
14	<i>Leanira yhleni</i> Mahngren	Polychaeta (Aphroditidae)	199
15	<i>Parcanassa mangeloides</i> Reeve	Gastropoda (Nassariidae)	185
16	<i>Lumbrineris latreilli</i> Audouin and Milne Edwards	Polychaeta (Eunicidae)	117
17	<i>Loimia medusa</i> (Savigny)	Polychaeta (Terebellidae)	108
18	tunicate 1	Ascidacea	105
19	tunicate 3	Ascidacea	101
20	bivalve 1	Pelecypoda	98
21	<i>Nucula astricta</i> Iredale	Pelecypoda (Nuculidae)	94
22	oyster 1	Pelecypoda (Ostreidae)	94
23	<i>Pectinaria antipoda</i> Schmarda	Polychaeta (Pectinariidae)	90
24	<i>Nereis jacksoni</i> Kinberg	Polychaeta (Nereidae)	90
25	<i>Mesochaetopterus</i> cf. <i>capensis</i> (McIntosh)	Polychaeta (Chaetopteridae)	90
26	<i>Ophelina gigantea</i> Rullier	Polychaeta (Opheliidae)	88
27	sea anemone 1	Actinaria	87
28	<i>Isolda pulchella</i> Müller	Polychaeta (Ampharetidae)	76
29	bivalve 2	Pelecypoda	74
30	<i>Tellina texturata</i> Sowerby	Pelecypoda (Tellinidae)	66
31	<i>Glycera prashadi</i> Fauvel	Polychaeta (Glyceridae)	62
32	<i>Cirriiformia</i> sp.	Polychaeta (Cirratulidae)	61
33	<i>Protankyra</i> sp.	Echinodermata (Holothuroidea)	61
34	<i>Petaloproctus terricola</i> Quatrefages	Polychaeta (Maldanidae)	55
35	bivalve 3	Pelecypoda	55
36	<i>Chama fibula</i> Reeve	Pelecypoda (Chamidae)	54
37	<i>Cycladicama</i> sp.	Pelecypoda (Ungulinidae)	53
38	balanid 1	Cirripedia	52
39	<i>Edwardsia</i> sp.	Actinaria	48
40	<i>Onuphis</i> sp.	Polychaeta (Eunicidae)	46
41	<i>Placamen sydneyense</i> Menke	Pelecypoda (Veneridae)	45
42	<i>Dasybranchus caducus</i> (Grube)*	Polychaeta (Capitellidae)	44
43	<i>Arca</i> sp. 1	Pelecypoda (Arcidae)	41
44	oyster 3	Pelecypoda (Ostreidae)	40
45	<i>Amphioplus depressus</i> (Ljungman)	Echinodermata (Ophiuroidae)	40
46	<i>Trichomya hirsuta</i> (Lamarck)	Pelecypoda (Mytilidae)	39
47	<i>Leptoniysa pura</i> Angus	Pelecypoda (Semelidae)	36
48	<i>Mesochaetopterus</i> sp.	Polychaeta (Chaetopteridae)	33

49	aphroditid 1	Polychaeta (Aphroditidae)	32
50	<i>Leonnates stephensoni</i> Rullier	Polychaeta (Nereidae)	31
51	<i>Clorida granti</i> (Stephenson)	Stomatopoda	30
52	<i>Marphysa sanguinea</i> (Montague)	Polychaeta (Eunicidae)	30
53	<i>Glossobalanus hedleyi</i> Hill	Enteropneusta (Balanoglossidae)	30
54	<i>Reticunassa paupera</i> Gould	Gastropoda (Nassariidae)	28
55	nemertean 'pink'	Nemertea	27
56	whip coral	Gorgonacea	27
57	<i>Venus</i> sp.	Pelecypoda (Veneridae)	26
58	<i>Macoma donaciformis</i> Deshayes	Pelecypoda (Tellinidae)	25
59	<i>Ophiactis perplexa</i> Koehler	Echinodermata (Ophiuroidae)	24
60	<i>Anomia</i> sp.	Pelecypoda (Anomiidae)	20
61	amphipod 4	Amphipoda	20
62	<i>Elamenopsis lineata</i> A. Milne Edwards	Decapoda (Hymenosomidae)	19
63	<i>Pista</i> sp.	Polychaeta (Terebellidae)	19
64	amphipod 2	Amphipoda	18
65	<i>Amacana trilobata</i> (Sars)	Polychaeta (Terebellidae)	18
66	<i>Hexapus granuliferus</i> Campbell and Stephenson	Decapoda (Goneplacidae)	18
67	tunicate 2	Ascidacea	16
68	<i>Chaetopterus variopedatus</i> Renier	Polychaeta (Chaetopteridae)	15
69	sabellid 1	Polychaeta (Sabellidae)	15
70	<i>Natica</i> sp.	Gastropoda (Naticidae)	14
71	amphipod 6	Amphipoda	14
72	<i>Tapes watlingi</i> Iredale	Pelecypoda (Veneridae)	13
73	amphipod 1	Amphipoda	12
74	<i>Bedeia hanleyi</i> Angus	Gastropoda (Muricidae)	12
75	<i>Brissopsis luzonica</i> (Gray)	Echinodermata	12
76	nemertean 'black'	Nemertea	11
77	<i>Modiolus 'ostentatus'</i> Swainson	Pelecypoda (Mytilidae)	11
78	ampharetid 1	Polychaeta (Ampharetidae)	11
79	<i>Paphia subrugata</i> Iredale	Pelecypoda (Veneridae)	10
80	<i>Eurythoe parvecarunculata</i> Horst	Polychaeta (Amphinomidae)	10
81	<i>Polydora</i> sp. 1	Polychaeta (Spionidae)	10

*Possible misidentification.

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INTRODUCTION OF THE NORTH ATLANTIC ASCIDIAN *MOLGULA MANHATTENSIS* (DE KAY) TO TWO AUSTRALIAN RIVER ESTUARIES

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ABSTRACT

Populations of the North American (Atlantic coast) *Molgula manhattensis* have been sampled at Newport Power Station in the mouth of the Yarra River, Victoria; and at several stations up to 22 kilometres from the mouth of the Brisbane River. The species and its affinities are discussed in detail, together with the implications of its distribution and its occurrence in Australian estuaries.

Eleven Stations in the Brisbane River, from its mouth to 70 km upstream, have been sampled by Mr R. Monroe at 3 monthly intervals from May 1974, following a major flood in January. In May 1975 two specimens (1.5 cm and 1.0 cm in diameter, respectively) of *Molgula manhattensis* were taken off Mowbray Park, some 16 km upstream. In August large numbers of the species were present at this site, and even larger numbers were taken up to 6 km further up the river in the South Brisbane Reach. By December only 3 specimens were taken at the latter station. Downstream, the species was taken only once, and in small numbers. The species was not present in samples taken in January 1976.

From May to August is the winter season of low rainfall and during that period highly seasonal populations of *Molgula* spp. are present in Moreton Bay (Kott 1972). *M. manhattensis* has not been taken in Moreton Bay, however, and it is most likely that parent stocks from which the riverine populations were recruited were located on shipping (from the western Atlantic via the Panama Canal) in the Port of Brisbane. This extends up the Brisbane River to within 3 km of the South Brisbane Reach.

In the family Molgulidae, it is known that sexual maturity is achieved early, in individuals of small size (Berrill 1931); while the spiral arrangement of stigmata in this family provides a means whereby maximum filtration area is available in small individuals to contribute to this general metabolic efficiency. Kott (1972) suggested that these factors would represent advantages where populations suffered seasonal mortality resulting from the periodic flooding, silt deposition, and temperature

fluctuations that commonly occur in sheltered bays. The large molgulid renal organ (see Berrill 1950) could also represent an advantage in these locations.

In fact, 7 of 12 free living ascidian species in Moreton Bay are molgulid species (Kott 1972); and *M. mollis* and *M. sabulosa* commonly occur in Port Phillip Bay (Kott, in press). Of 29 species reported on from America (Van Name 1945) 7 are recorded from harbours, estuaries, and river mouths; 6 are recorded from intertidal or shallow waters; and 11 occur in shallow waters in polar regions where melting ice causes seasonal dilution of sea water.

Molgula manhattensis (de Kay) and the closely related *M. tubifera* (Orsted) appear to have developed the capacity to withstand brackish conditions to a surprising extent. The combined records of both species (*> M. manhattensis*: Thompson 1930; Berrill 1950) range 'from the White Sea to the tropics in water whose salinity varies from 16 to over 30‰' (Thompson 1930, p. 23). Berrill (1950, p. 248) has also commented on their tolerance of the 'diluted and polluted waters typical of estuaries and harbours'. Van Name (1945, p. 388) refers to the western Atlantic *M. manhattensis* as 'one of the few ascidians that will live in water of somewhat diminished salinity'.

It is not altogether surprising, therefore, that it is *M. manhattensis* which has been introduced into Brisbane River, some 22 km from its mouth, where the bottom salinity (registered at the Port Office, in the Town Reach of the river, between the stations sampled off Mowbray Park and in the South Brisbane Reach) was in the vicinity of 16‰ in

May 1975; 19‰ in August 1975; 25‰ in September 1975; and 11‰ in December 1975.

It is not impossible that there have been earlier introductions that were eradicated by the January 1974 flood. It is also possible that introduced riverine populations do not withstand the summer rainfall period and that, unless the species has become established in refuges in Moreton Bay, subsequent recruitment (if any) will also be from ships hulls.

Apart from the fact that *Molgula manhattensis* of 1.2 cm diameter from Woods Hole in September 1927 had attained sexual maturity (Berrill, 1931), little is known of the growth rate and breeding season of *M. manhattensis* and this must be largely inferred from what is known of related species. *M. tubifera* (closely related to *M. manhattensis*) has been found breeding at Plymouth in all seasons other than winter (March to October; Berrill 1931, 1935). *Molgula mollis* (> *M. sabulosa*; Kott, 1972) is a species of similar size which reaches sexual maturity before reaching 2 cm in diameter. After settling in Moreton Bay at the end of winter, this species apparently produced at least one generation of offspring which grew to at least 2 cm in diameter before the populations disappeared in summer (Kott 1972). Therefore, sexual maturity is apparently attained within 2 months. If the growth rate and breeding season of the introduced populations of *M. manhattensis* are comparable with

these, juveniles settling on ships in the western Atlantic in autumn could have been transported to the southern hemisphere, where their offspring settled in the Brisbane River following the period of summer rain (March 1975). Then the large mature populations sampled in August would have been adults of the second generation, progeny of the parent generation that settled in the river to reach sexual maturity in May; and the individuals taken in October would represent a third generation.

***Molgula manhattensis* (de Kay, 1843)**
(Figs. 2–4)

Ascidea manhattensis De Kay, 1843, p. 259.

Molgula manhattensis: Van Name, 1945, p. 385 and synonymy.

Molgula platei: Arnback, 1928, p. 22, plate 1, figs. 31–4.

NEW RECORDS

Brisbane R.: QM G8976, G8977, G8979 Mowbray Park (32 specimens, R. Monroe, 7.viii.1975); QM G8978, mud channel, mouth of Norman Creek (2 specimens, R. Monroe, 12.v.1975); South Brisbane Reach, below Executive Building (numerous specimens, R. Monroe, 7.viii.1975; 50 specimens including juveniles, R. Monroe, 30.x.1975; 3 specimens, P. Davies, 5.xii.1975); Bulimba corner (1 specimen, R. Monroe, 30.x.1975).

Yarra R.: NMV H301, Newport Power Station (9.i.1967).

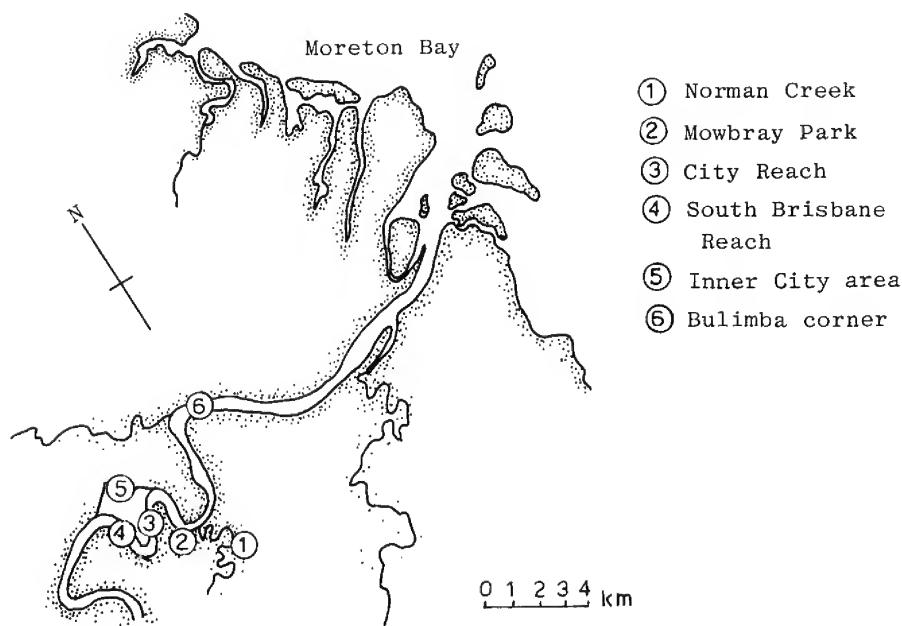


FIG. 1: Lower Reaches of the Brisbane River from the Inner City area to Moreton Bay.

OTHER MATERIAL EXAMINED

Molgula tubifera: AM Y1949, Duke Rock, Plymouth, U.K. (2 specimens, P. Kott, July 1951).

DISTRIBUTION

On the Atlantic coast of North America from Portland to Louisiana (Van Name 1945). *M. platei* Hartmeyer, 1914; Van Name, 1945, known only from a single specimen from Chile, is similar to the present species. If closer examination should prove them synonymous, the possibility that it had been transported between the Pacific and Atlantic coasts of America, by ship, should not be overlooked.

The species is commonly taken from shallow waters, the deepest reliable record being at 30 m (Van Name 1945).

DESCRIPTION

Individuals are almost spherical, to ovoid, slightly laterally flattened, and up to 2.5 cm in diameter. Both apertures are on short siphons a short distance apart on the upper surface. The branchial aperture is turned ventrally and the atrial aperture diverges slightly in the opposite direction. The test is whitish, thin, papery and transparent. It is covered with sparse, short hairs to which mud and fine sand adhere. On the basal half of the body the hairs are longer and form root-like processes anchoring the animal into the substrate. (Fig. 2).

The body wall is very thin with muscles conspicuous only around the siphons. It is very closely adherent to the test. At the base of the branchial siphon there is a straight edged velum on both sides which reduces the opening to a longitudinal slit. Longitudinal muscles from the body wall extend into these velar folds of the siphonal lining. The branchial tentacles are very bushy. The dorsal tubercle is a circular cushion with a U-shaped opening turned posteriorly, the horns turned inwards. The dorsal lamina is very short and is joined by 3 broad transverse vessels from each side of the body.

The branchial sac has 6 narrow deeply curved folds on each side of the body. There are no internal longitudinal vessels between the folds. Those on the folds are extremely broad and project out from the ventral surface of the fold as a flat membrane. The internal longitudinal vessels become progressively wider toward the base of each fold. There are no internal longitudinal vessels on the dorsal surface of the fold. Longitudinal vessels on the ventral surface of each fold are arranged according to the formula DL 0(3) 0(4) 0(4) 0(4) 0(3) 0 E. In the very extensive spaces between the folds there are very numerous, and irregular, interstitial in-

fundibula, with interrupted and irregular vessels extending across them (Fig. 3). The primary infundibula in each fold are subdivided into two and each subdivision is again divided at its apex in the margin of the fold. However, this arrangement is much obscured by the many irregular accessory or interstitial coils that are present, especially near the apex of the coils. In older specimens there is an unperforated area along either side of the endostyle.

The gut forms a very narrow deeply curved loop enclosing the gonad on the left side of the body. The stomach is long, with internal longitudinal glandular folds. The anal border is divided into about 12 shallow rounded lobes. On the right side the molgulid kidney occupies the usual postero-ventral position. It is long and slightly curved and increases in length as the individual becomes larger. The right gonad extends along parallel to the dorsal border of the kidney. The gonads consist of an elongate or flask-shaped ovary terminating postero-dorsally in a short oviduct. Very dense clumps of arborescent testis follicles are arranged continuously along the proximal end and the ventral border of each ovary. Only occasionally there are small isolated clumps of testis follicles on the dorsal margin of the ovary. Vasa efferentia extend from the testis follicles onto the mesial surface of the ovary where they unite into one short vas deferens on the right gonad, but on the left gonad there are up to six short vas deferens arranged along the length of the ovary. (Fig. 4).

Occasionally eggs, with follicle cells, are found in the peribranchial cavity, but no larvae were found suggesting that the species is oviparous. The eggs are 1.1 mm in diameter, excluding the follicle cells. Juveniles were present attached to the test of adult specimens in August.

RELATIONS

Hartmeyer (1923) and Berrill (1950) believe the European *M. tubifera* to be synonymous with *M. manhattensis*. Hartmeyer's synonymy is based on the fact that the gut loop of both *M. tubifera* and *M. manhattensis* is equally narrow and deeply curved and encloses the left ovary. Berrill's view is supported by the small eggs and oviparous habit and similar development in both species (Berrill 1928).

Despite similarities between the species, neither Arnback (1928) nor Van Name (1945) accepted the synonymy of *M. tubifera* and *M. manhattensis*. Arnback points out that the branchial sac of European specimens has fewer accessory spirals than *M. manhattensis*.

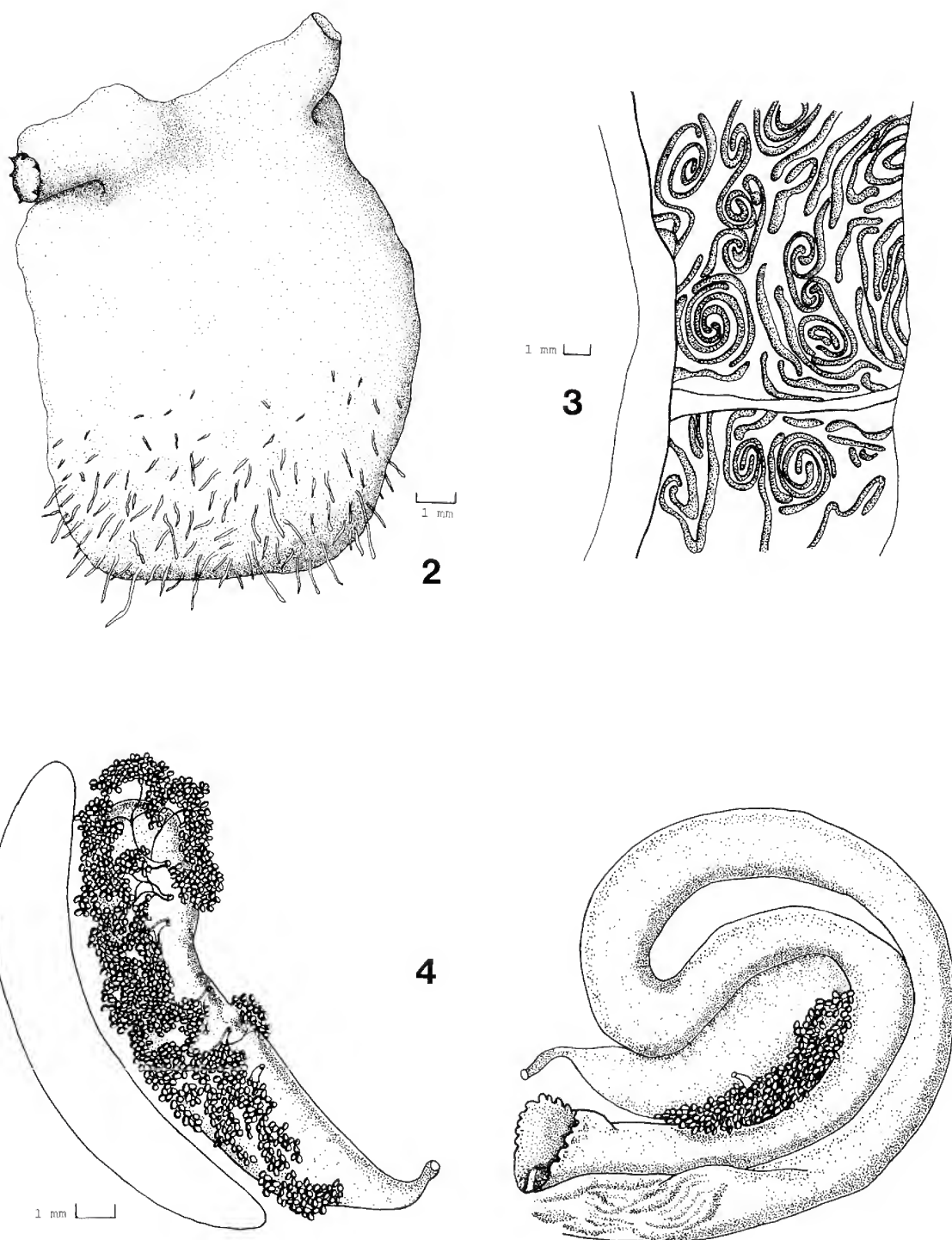


FIG. 2: *Molgula manhattensis*; external appearance (specimen from the Brisbane River).

FIG. 3: *Molgula manhattensis*; portion of branchial sac between the folds (specimen from the Brisbane River).

FIG. 4: *Molgula manhattensis*; kidney, gut and gonads on inner body wall (specimen from the Brisbane River).

Specimens from the English Channel in the collection of the Australian Museum (AM Y1949, Duke Rock, Plymouth, July 1951) have been re-examined. They resemble the present specimens of *M. manhattensis* from the Brisbane River in size and general appearance, in the number of branchial folds, in the deeply curved gut loop, in the position of the right gonad parallel to the kidney, and in the size of the eggs and testis follicles. The differences between the American *M. manhattensis* and the European *M. tubifera* are confirmed, however, and the details of these differences are set out in Table 1.

The multiplicity of short testis ducts in the present specimens from the Brisbane and Yarra Rivers is similar to that inferred for *M. manhattensis* by Huntsman, 1922, and that known for some specimens of the European species (see Arnback 1928). However, Arnback (*loc. cit.*) has drawn attention to variations in the condition of the vas deferens in a range of specimens from European locations.

The multiple short vas deferens found in *M. manhattensis* and related species was used by Huntsman (1922) to characterise the genus *Gymnocystis*. Based on this criterion *M. ampulloides* (a synonym of *M. tubifera*) was excluded from that genus.

Huntsman's subdivision of the genus *Molgula* was not adopted, however, since variations in arrangement of testis follicles relative to the ovary and variations in the length and disposition of the vas deferens occur throughout the genus, and are not considered to be of more than specific

significance. The significance of this reported variation in the condition of the vas deferens in *M. tubifera* and its synonyms has yet to be resolved.

In the Australian Museum specimens from the English Channel, referred to above, a single vas deferens extends along the mesial surface of the ovary and opens near the opening of the oviduct.

The Brisbane and Yarra River specimens conform exactly in all respects with the American species *M. manhattensis* (see Van Name 1945).

Table 2 sets out the principal characters which distinguish those species in which more than a single vas deferens associated with the right or left gonad has been reported.

FILTRATION RATE

The capacity of the individual to filter large amounts of water and deal effectively with the sediments filtered from the water could also be relevant to its occurrence in shallow estuaries and in other locations where there is an unusual amount of suspended matter and other pollutants.

The pronounced branchial folds of *M. manhattensis* and the complex arrangement of primary and accessory infundibula on the folds and in the interspace have developed the area available for filtration to a maximum degree.

MacGinitie (1939) and Day (1974) have shown that in *Ascidia californica* and *Pyura stolonifera* respectively, mucous moves over the pharynx in a continuous sheet. Jorgensen's (1939) assessment of filtration rate of *Molgula manhattensis* and *Ciona intestinalis* suggests that all particulate matter

TABLE 1: DIFFERENCES BETWEEN *M. manhattensis* AND *M. tubifera*

Species	Apertures	Internal longitudinal vessels/fold	Testis follicles	Dorsal tubercle	Stigmata	Anal border
<i>M. manhattensis</i>	close together on the upper surface; long when extended (see Arnback 1928, fig. 34)	never exceeds 4; present on dorsal side of fold only	not present on dorsal border of ovary	cup-shaped with unrolled horns turned to the right or posteriorly	numerous accessory spirals; long stigmata (see also Van Name 1945)	lobed
<i>M. tubifera</i>	a little distance apart on the upper surface; moderate length when extended (see Thompson 1930, pl. 3, figs. 1, 2)	up to 7 (Thompson 1930, p. 21; '3 to 6 mostly' 5 to 6); present on both sides of fold	present all around ovary	slit-like, S-shaped, C-shaped or U-shaped or turned to the right, or left or posteriorly (Arnback 1928)	only occasional accessory spirals; stigmata short (see also Thompson 1930, pl. 3, fig. 6)	smooth

TABLE 2: COMPARISON OF *Molgula* spp., WITH DEEPLY CURVED GUT LOOP AND MULTIPLE VAS DEFERENS

Species	Gut loop curve	Accessory infundibula; stigmata	Branchial folds	Maximum number longitudinal vessels/fold	5 follicles	Range	Reference to description
<i>M. herdmanni</i> Bjerkn	shallow	rare; long	7; pronounced	7	surround ovary	Norway	Arnback, 1928
<i>M. robusta</i> Van Name	deep open	rare; short	6; pronounced	11	surround ovary	Massachusetts	Van Name, 1945
<i>M. siphonalis</i> Sars	deep open	rare; long	7; pronounced	7	surround ovary	N. Atlantic	Van Name, 1945
<i>M. provisionalis</i> Van Name	deep open	rare; long	6; low	8	surround ovary	N.W. Atlantic	Van Name, 1945
<i>M. macro-siphonica</i> Kupffer	deep open	rare; short, irregular	6; low	?	surround ovary	Baltic North Sea	Arnback, 1928
<i>M. tubifera</i> Orsted	C-shaped	occasional; short	6; pronounced	8	surround ovary	N.E. Atlantic	Arnback, 1928
<i>M. munhattensis</i> de Kay	C-shaped	numerous; long	6; pronounced	4	along ventral border of ovary	N.W. Atlantic	see above
<i>M. calvata</i> Sluiter	deep open	none; long	7; low	2	surround ovary	Indonesia N.E. Aust. S.W. Aust.	Kott, 1964

(down to 1 micron at least) is strained from the water by this sheet of mucous.

It was possible, therefore to estimate an approximate rate at which *Molgula manhattensis* filtered the muddy water of the Brisbane River.

The filtration rate was assessed according to the formula:

$$m = \frac{(\log \text{conc}_0 - \log \text{conc}_t) \times M}{\log e \times t}$$

where m is the quantity of water filtered in time t; conc_0 is the concentration of particles in the water at the beginning of the experiment and conc_t is the concentration of particles in the water at the end of the experiment; t is the duration of the experiment; and M is the amount of water in the experimental vessel (see Jorgensen 1943).

The present experiment was conducted for a period of 12 hours with duplicate specimens of *M. manhattensis*, each in 1.3 litres of Brisbane River water with a heavy suspension of fine mud. No sedimentation had occurred in the control vessel at the end of the experiment. The concentration of particles in suspension after 12 hours is expressed as a percentage of the concentration at the beginning of the experiment, and was estimated by measured dilution of the unfiltered water to match opacity observed in the experimental vessels at the end of the experiment. The dilution achieved by the removal of suspended particles by the ascidian, over this 12 hour period was of the order of 1 in 1000.

The filtration rate of a single specimen of *Molgula manhattensis* was thus shown to be in the vicinity of 1.25 mls/minute (750 mls/hour). This rate confirms Jorgensen's (1952) values of 8 to 18 litres per hour for 15 specimens.

These small individuals are, therefore, very efficient filter feeders. The capacious and long gut loop with its pronounced typhlosolar fold undoubtedly contributes to the accommodation of large amounts of sediment from which nutriment is extracted.

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UPPER MOLAR ALVEOLAR PATTERNS OF SOME MURIDAE IN QUEENSLAND AND PAPUA NEW GUINEA

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SUMMARY

The upper molar alveolar patterns of 33 species in 16 genera of Muridae are illustrated. The eight patterns recognized are each related to a genus or a group of genera; the taxonomic value of the patterns is limited because of inconsistent, though infrequent, variation. Although patterns do not distinguish among native *Rattus* species, they provide a useful additional criterion for separating *Melomys cervinipes* (Gould) from *Melomys littoralis* (Lönnberg).

Biological entities within the Muridae remain ill-defined despite a voluminous literature in the medical, agricultural and pure zoological fields. During long-term studies of *Rattus* and *Melomys* in Queensland, attention was given to the taxonomic value of alveolar patterns in the maxillae. Jones (1922) described the alveolar patterns of five species of murids from South Australia, and Ellerman (1942) discussed the roots of M¹ of Australasian Muridae. With the expansion of field work throughout Queensland to Cape York Peninsula, exploratory efforts were made with other genera in Queensland and some species from Papua New Guinea.

MATERIAL EXAMINED

Rattus and *Melomys* specimens were available in numbers (see Table 1) from recent field collections throughout the State and from consequent breeding colonies. The collections of the Department of Forestry and the Queensland Museum (QM) were examined also. Skulls were selected from the available material. *Hydromys* specimens were readily available; skulls of *Conilurus albipes* (Lichtenstein) were used because a Queensland specimen of *C. penicillatus* (Gould) was not available.

The Australian Museum (AM) provided a skull of *Xeromys myoides* Thomas from Mackay, Q., and a skull of *Melomys lutillus* (Thomas) from Papua New Guinea. The University of Queensland supplied specimens of *M. rufescens* (Alston) (type species), *Pogonomelomys sevia* (Tate and Archbold), and *Pogonomys mollipilosus* Peters and

Doria, also from Papua New Guinea. All other specimens, except those from recent field collections presently retained by the Queensland National Parks and Wildlife Service, Brisbane, are in the Queensland Museum.

Nomenclature is based on Iredale and Troughton (1934).

ALVEOLAR PATTERNS

Alveolar patterns of the 33 species examined are shown in Plates 61-2. The distribution of alveoli among molars falls into eight patterns which, with related genera, are set out in Table 1. *Melomys* (Group A) consists of *M. lutillus*, *M. littoralis*, and *M. australis*; *Melomys* (Group D) of *M. cervinipes*, *M. rufescens*, *M. rubicola*, and *Melomys* sp. The patterns for *Rattus*, *Hydromys*, *Mus*, and *Notomys* agree with those of Jones (1922).

The plates also illustrate variations seen in the patterns recorded in Table 1. The irregular shape of a large alveolus is frequently the result of a union with an adjacent small one; this becomes apparent when the third molar is fully erupted and a permanent pattern is discernible, as is illustrated by Plate 62Da. Occasionally an alveolus of comparatively small size and variable location may occur (Plate 61E); such aberrations are rare, being present for example in less than 1% of the series of *M. cervinipes*.

The taxonomic value of the alveolar patterns is limited because of the inconsistent variation that occurs infrequently within these. This study thus did not assist in distinguishing species of native

Rattus, but the occurrence of two patterns in *Melomys* (Table 1A and D) provides a morphological character, independent of age and of measurements, which is a useful additional criterion for separating *M. cervinipes* and *M. littoralis*.

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Queensland Museum, permitted the use of its reference collection. Mr P. Fry, formerly Photography Branch, Department of Primary Industries, provided all of the illustrations. This assistance is gratefully acknowledged.

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TABLE 1: MOLAR ALVEOLAR PATTERNS AMONG 16 MURID GENERA

Pattern	Distribution of molar alveoli			Genus (specimens examined)
	M ¹	M ²	M ³	
A	5	5	3	<i>Melomys</i> (120)
B	5	4	3	<i>Rattus</i> (90)
C	5	3		<i>Hydromys</i> (5), <i>Xeromys</i> (1)
D	4	4	3	<i>Uromys</i> (6), <i>Melomys</i> (180), <i>Pogonomys</i> (6)
E	4	3	2	<i>Conilurus</i> (2)
F	3	3	3	<i>Mus</i> (3), <i>Pseudomys</i> (18), <i>Mesembriomys</i> (2), <i>Zyzomys</i> (2), <i>Thetomys</i> (2), <i>Pogonomelomys</i> (6)
G	3	3	3*	<i>Gyomys</i> (2)
H	3	3	2	<i>Leggadina</i> (5), <i>Notomys</i> (7), (<i>Leporillus</i> †)

*arrangement different from Pattern F (cf. Plate 62 F a)

†after Jones (1922)



PLATE 61

Right maxillae, showing alveolar patterns A, B, C, E, and G.

Pattern A

- a, *Melomys lutillus* (Thomas) AM M6925
- b, *Melomys littoralis* (Lönnberg)
- c, *Melomys australis* Thomas

Pattern B

- a, *Rattus norvegicus* (Erxleben)
- b, *Rattus rattus* Linnaeus
- c, *Rattus lutreolus* (Gray)
- d, *Rattus assimilis* (Gould)
- e, *Rattus leucopus* (Gould)
- f, *Rattus villosissimus* Waite QM J22613
- g, *Rattus culmorum* (Thomas and Dollman)
- h, *Rattus conatus* Thomas

Pattern C

- a, *Hydromys chrysogaster* Jeffroy
- b, *Hydromys longmani* Thomas QM J3784, Paratype
- c, *Xeromys myoides* Thomas AM M6529

Pattern E

Conilurus albipes (Lichtenstein) QM J3348

Pattern G

Gyomys berneyi Troughton QM J14755

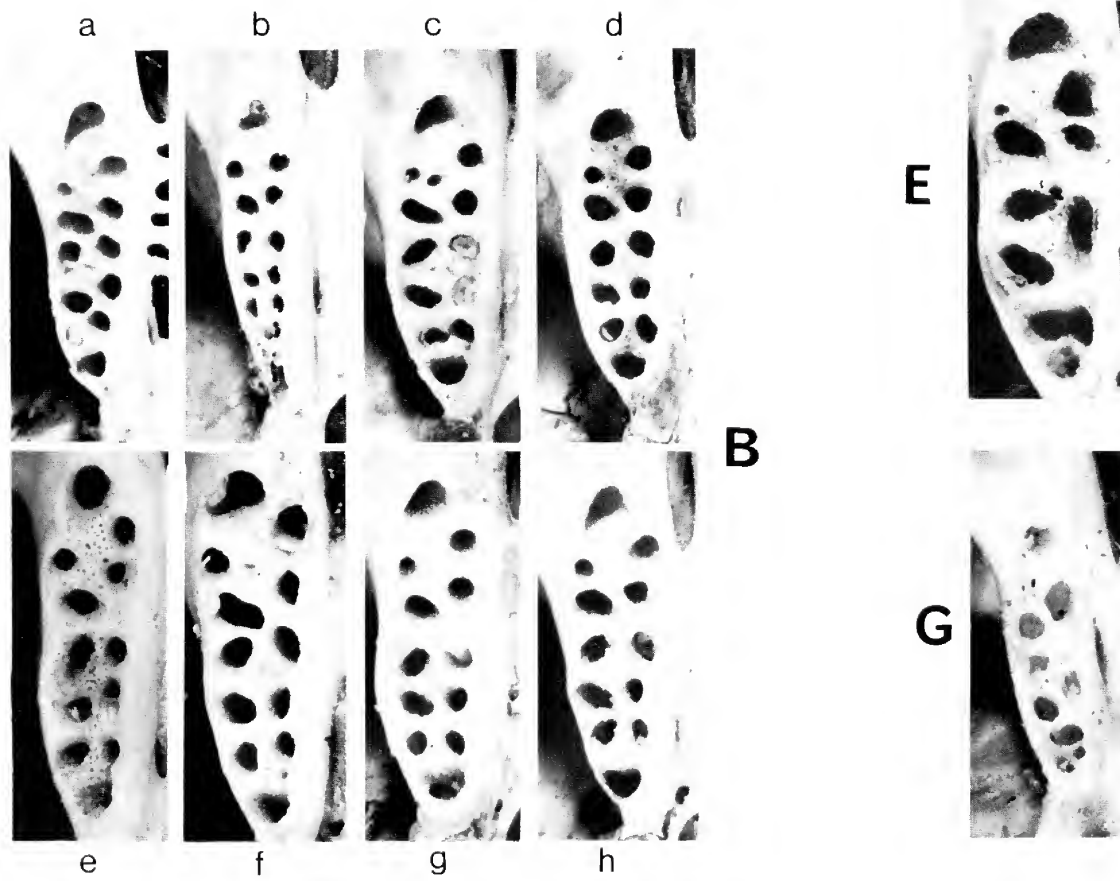
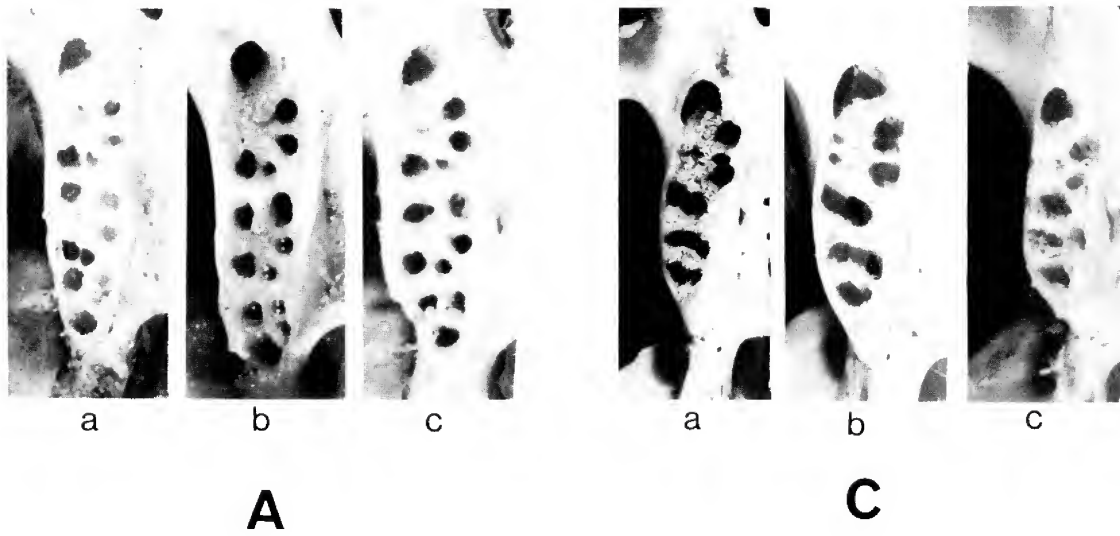


PLATE 62

Right maxillae, showing alveolar patterns D, F, and H.

Pattern D

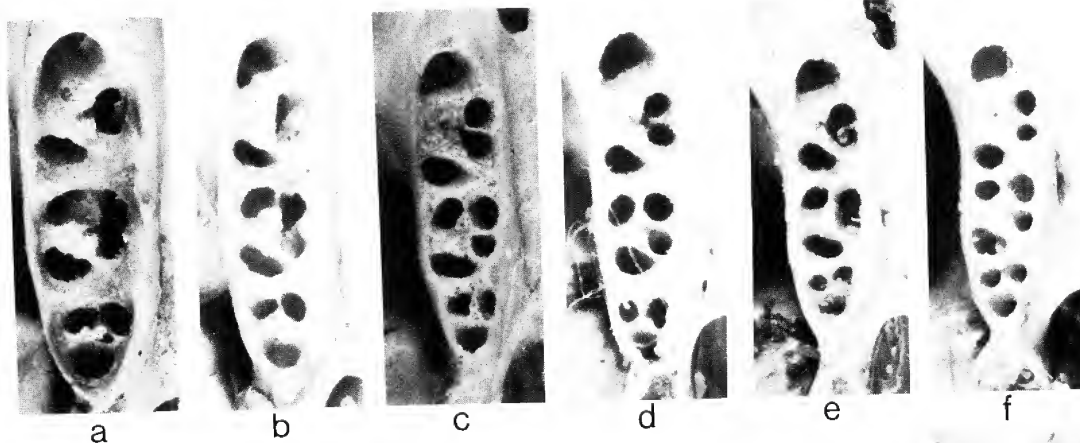
- a. *Uromys caudimaculatus* (Krefft) QM J22540
- b. *Uromys sherrini* Thomas QM J3785 Paratype
- c. *Melomys cervinipes* (Gould)
- d. *Melomys rufescens* (Alston)
- e. *Melomys rubicola* Thomas QM J20169
- f. *Melomys* sp.
- g. *Pogonomys mollipilosus* Peters and Doria

Pattern F

- a. *Mus musculus* Linnaeus QM J2991
- b. *Pseudomys novaehollandiae* (Waterhouse) QM J17920
- c. *Pseudomys oralis* Thomas
- d. *Pseudomys minnie* Troughton QM J5944
- e. *Mesembriomys gouldii* (Gray) QM J16978
- f. *Zyomys argurus* (Thomas) QM J22401
- g. *Thetomys gracilicaudatus* (Gould)
- h. *Pogonomelomys sevia* (Tate and Archbold)

Pattern H

- a. *Leggadina delicatula* (Gould) QM J16468
- b. *Notomys filmeri* Mack QM J10009



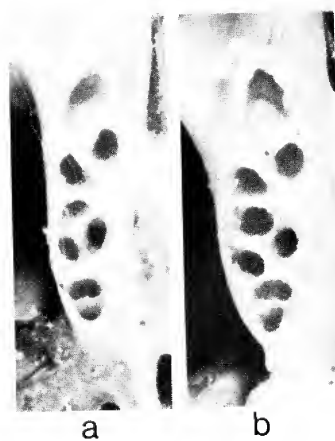
D



F



H







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